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THE ECOLOGY AND BEHAVIOUR OF THE RUDDY DUCK *Oxyura jamaicensis jamaicensis* (Gmelin) IN GREAT BRITAIN

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ABSTRACT

The Ruddy Duck *Oxyura jamaicensis* is native to North America. It was introduced into Great Britain in 1952, bred for the first time in 1960 and is now widespread. The British population now numbers some 3500 birds and is increasing at about 10% per year. This project aimed to determine what interactions occur between introduced Ruddy Ducks and native British species of bird through a detailed study of their behaviour throughout the year.

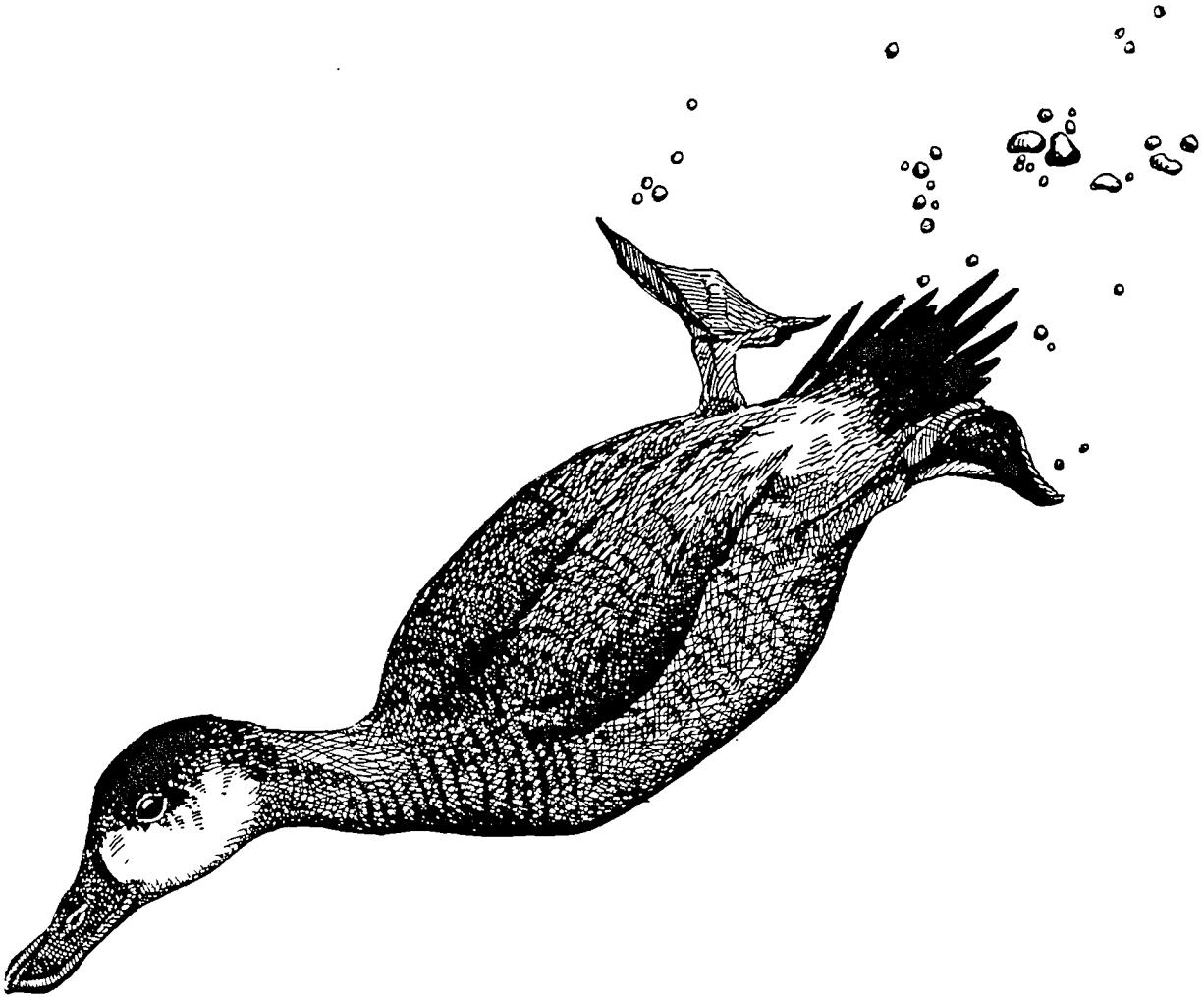
The introductory chapter reviews the history of the Ruddy Duck in Great Britain. Chapter 2 then describes the behaviour and diving activity of Ruddy Ducks at Chew Valley Lake, Avon. Birds fed mainly at night and spent 70% of the day resting. Males in alternate plumage, males in basic plumage and females/juveniles behaved similarly during the day, but at night females/juveniles fed more and swam less than males. A lunar rhythm of activity depending on prey activity/availability is suggested to explain observed behavioural trends. The effect of weather on behaviour is also considered.

The diurnal activity of courting male and brood female Ruddy Ducks at Mere Sands Wood Nature Reserve, Lancashire is described in chapters 3 and 4. Courting males spent 51% of the day feeding, 26% swimming and 15% resting. The males' behaviour differed between three sites of observation whilst paired status affected their behaviour on only one. The effect of the presence of other Ruddy Ducks, time of day, date and temperature on activity is then assessed. Brood females spent most time swimming, feeding and resting whilst allocating 5% of their time to alert behaviour and 5% to parental care. The activity of individual females differed in response to a number of biotic and physical factors. As ducklings aged, resting and swimming behaviour remained relatively constant whilst comfort movements tended to increase and feeding and parental care tended to decline. The mechanism of brood desertion appeared to be controlled by a combination of increasing duckling independence and decreasing female attentiveness. The effect of time of day and temperature on brood female activity is discussed.

Diurnal social interaction of Ruddy Ducks is assessed in chapter 5. The majority of social interactions were intraspecific throughout the year. The rate of intraspecific interaction was very low in winter, higher in courting males and highest in brood females. The rate of interspecific interaction was very low in wintering birds, but brood females showed the highest rate of interaction of all ducks or coot. Although courting males showed a low rate of interspecific interaction, they initiated and won most interactions. Paired male Ruddy Duck initiated and won a higher proportion of interactions than unpaired males. Trends in courting male social interaction with time of day and date are discussed in relation to the social structure which exists during courtship. The number and intensity of brood female social interactions tended to decrease with increasing brood age whilst time of day had little effect on brood female social interaction.

At the present population level it appears that introduced Ruddy Ducks are exploiting an available niche in the British wetland ecosystem and are, therefore, having little effect on native waterbirds. However, the apparent interspecific dominance of courting males, the high level of interspecific interaction in brood females and the similar breeding requirements of Ruddy Ducks and native species of grebe do give some cause for concern. The Ruddy Duck is now beginning to colonise the European mainland and there is already evidence that it may threaten the existence of the White-headed Duck through competition and hybridisation. In response the steering committee for the EC birds directive passed a motion in March 1992 that the United Kingdom and Spain take immediate action to control the Ruddy Duck.

I would like to dedicate this Ph.D. to the late Sir Peter Scott,
the founder of The Wildfowl & Wetlands Trust.



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I am extremely grateful to my supervisors, Myrfyn Owen and Roger Avery, who provided invaluable assistance and support and, finally, I would like to thank Philippa Scott for allowing me to dedicate this Ph.D. to Peter.

I declare that the work contained in this thesis is all my own and has not been produced in collaboration with, or with the assistance of, any other person except in an advisory capacity.

The views expressed in this dissertation are my own, not those of Bristol University.

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CHAPTER ONE.

GENERAL INTRODUCTION. The history of the Ruddy Duck *Oxyura jamaicensis* (Gmelin) in Great Britain: past and present status and distribution.

The Ruddy Duck *Oxyura jamaicensis* (Gmelin, 1789) is one of five species of stifftail ducks comprising the genus *Oxyura*. It is native to North and western South America and occurs from Alaska in the north to Tierra del Fuego in the south. There are three subspecies of Ruddy Duck: the North American Ruddy Duck *O. j. jamaicensis*, which breeds in the United States of America (U.S.A.) and Canada and winters in coastal and southern U.S.A. and in Mexico, the Peruvian Ruddy Duck *O. j. ferruginia*, which occurs on high altitude lakes in the Andes from southern Colombia to Tierra del Fuego, and the Colombian Ruddy Duck *O. j. andina* which occurs in the central and eastern Andes of Colombia.

In the past, the nominate subspecies has been separated into two subspecies, *O. j. jamaicensis* (Gmelin) from the West Indies and *O. j. rubida* (Wilson) from North America (Palmer 1976), but this division was not recognised by Scott (1988) or Cramp and Simmons (1977) and, for that reason, not recognised in this study. The name "Ruddy Duck" used throughout this thesis refers to the nominate subspecies *O. j. jamaicensis.*

Ruddy Ducks are essentially aquatic birds, flying rarely except during migration. They breed on freshwater marshes where nests are built over shallow water in dense emergent vegetation. In North America, they winter either on the coast or on inland lakes whereas in Britain they winter almost exclusively on large lakes or reservoirs with natural shorelines. Migration in Great Britain is limited to a relatively short seasonal movement between breeding areas in central and northern Britain and wintering grounds further south. Ruddy Ducks mainly feed on aquatic invertebrates, especially Chironomid larvae, but may take plant material occasionally.

Ruddy Ducks were first kept in captivity in Great Britain by Mr Noel Stevens at Walcott Hall, Shropshire, but this collection became dispersed during the Second World War (Lever 1977). In autumn 1948, The Wildfowl Trust imported three pairs of Ruddy Ducks and one single male from a collection in Salt Lake City, Utah. One pair of birds attempted to breed in 1949, but were not successful. Two pairs bred the following year

and 20 young were raised. Over the next few years, young birds proved difficult to hand-rear so, from 1955, the majority were left to be reared by their parents. However, due to the difficulty in catching parent-reared ducklings, the majority of these birds were not pinioned and were, therefore, left full-winged. The first full-winged birds escaped from Slimbridge in early 1953 and a further 90 birds are believed to have escaped up to 1973 (Hudson 1976). In addition, birds are known to have been reared full-winged at a private collection at Monken Hadley, Hertfordshire (Lever 1977). In recent years, it is safe to say that the number of birds which have escaped from Wildfowl & Wetlands Trust (WWT) centres has been negligible, but it is impossible to quantify the number of escapees from other private waterfowl collections.

Soon after the first birds escaped from Slimbridge, separate populations became established in Avon and Staffordshire. Feral breeding first occurred in Avon at Chew Valley Lake (CVL) in May 1960 (King 1976) and, in Staffordshire, at both Gailey and Belvide Reservoirs in 1961 (Harrison 1982). In the following years, the West Midlands became established as the major breeding area for Ruddy Ducks in Great Britain and, as the Ruddy Duck had established a self-sustaining feral population by 1971, it was admitted to the British and Irish list (British Ornithologists' Union 1971). Although the stronghold of the breeding population remains in the West Midlands, there are now notable concentrations in Cheshire, Greater Manchester, Lancashire, Yorkshire and on Anglesey. During the 1980's, the breeding range of the Ruddy Duck expanded, mainly northwards, and birds now breed regularly in the Fife and Tayside regions of Scotland, and sporadically in the Strathclyde and Grampian regions (Hogg 1989; Wood 1991; Buckland et al 1990; H. Bell in litt.; A. Brownhall in litt.; S.R. Hacker in litt.). Small numbers also regularly breed in Northern Ireland and the Irish Republic (Hutchinson 1989; C. Mellon pers. comm; O. Merne pers. comm.).

There has been no recent breeding survey of Ruddy Ducks in Great Britain, but if the post-breeding population (see below) is assumed to be six times the number of breeding pairs (Owen *et al* 1986), the breeding population in 1990 can be estimated at 570 pairs (Hughes in prep.). Following breeding, Ruddy Ducks may undergo the pre-basic moult on the breeding grounds (R. King pers. comm.) or fly to moulting sites, such as Belvide Reservoir, Staffordshire.

Until recent years, the main wintering areas have been in the Midlands and Avon. Blithfield Reservoir, Staffordshire and CVL have been the major sites, although recent mild winters have allowed the majority of the Ruddy Duck population to remain at more northerly sites, nearer to the main breeding grounds, with Rutland Water, Leicestershire holding more birds than CVL in the winter of 1990/91. Figure 1.1 illustrates the above information and highlights the expansion of the winter distribution of Ruddy Ducks in Great Britain between the winters of 1977/78 and 1990/91. The increased winter distribution is also illustrated by the fact that whereas Ruddy Ducks had been recorded from 135 sites up to 1978/79 (Owen *et al* 1986), this had increased to over 500 by 1990/91. In addition, Ruddy Ducks have now been recorded in every county in England and Wales and most regions in Scotland. Sightings of Ruddy Ducks range throughout Great Britain from Kent and the Scilly Isles in the south to the Outer Hebrides and the Shetland Isles in the far north of Scotland.

It is possible to obtain a reasonable estimate of the British population of Ruddy Ducks from winter counts because of the birds gregarious habits at this time of year. For example, in January 1991, the top ten sites for Ruddy Duck in Great Britain held approximately 83% of the total British population. Data from the WWT's National Waterfowl Counts (NWC) reveals the dramatic increase in the size of the British wintering population of Ruddy Ducks (Table 1.1 and Fig. 1.2). Differences between Table 1.1 and the same table in Hughes (1991) are due to recent corrections made to the NWC database. In the period 1965-75 numbers increased by about 25% per annum (Owen *et al* 1986) and continued to rise at between 6.3% and 109.6% p.a. until the winter of 1981/82 when there was a 17.2% decline in the numbers of birds counted.

Owen *et al* (1986), probably quite rightly, explained this decline in terms of hard weather mortality. However, the situation concerning hard weather mortality is not clear cut. Vinicombe and Chandler (1982) described the movements of British Ruddy Ducks during the hard winter of 1978/79 and suggested that there was a mortality of 5-10% between December 1978 and February 1979. However, there was actually a 45.6% increase in the maximum monthly count of Ruddy Ducks the following winter (Table 1.1). This may suggest that:-

1. The mortality was real and mainly included birds of non-breeding age.

TABLE 1.1. Annual totals of Ruddy Ducks in Great Britain. Figures up to 1975/76 from Hudson (1976), assuming that the ratio of pairs to post-breeding population was similar to that in 1975, when population = pairs x 6). Figures after 1975/76 are the maximum monthly count (to nearest 10 birds) from National Waterfowl Counts. a - Figures after 1975/76 calculated from National Waterfowl Counts, assuming a 90% count efficiency (Owen *et al* 1986). H denotes hard winter.

Winter	Maximum Count (Month)	% Change from Previous Year	GB Population Estimate [a]
61/62			18
62/63 (H)		+100.0	36
63/64		-33.3	24
64/65		0.0	24
65/66		+50.0	36
68/69		+66.6	60
71/72		+100.0	120
73/74		+75.0	210
74/75		+28.6	270
75/76		+29.6	350
76/77	430 (Oct)	+37.1	480
77/78	460 (Dec)	+6.3	510
78/79 (H)	510 (Mar)	+11.8	570
79/80	750 (Jan)	+45.6	830
80/81	1570 (Feb)	+109.6	1740
81/82 (H)	1300 (Nov)	-17.2	1440
82/83	1420 (Jan)	+9.7	1580
83/84	1820 (Dec)	+27.8	2020
84/85 (H)	1810 (Nov)	-0.1	2010
85/86 (H)	2030 (Jan)	+12.4	2260
86/87 (H)	2080 (Dec)	+2.2	2310
87/88	2320 (Jan)	+11.7	2580
88/89	2460 (Jan)	+5.8	2730
89/90	2850 (Jan)	+16.1	3170
90/91	3080 (Jan)	+7.9	3420

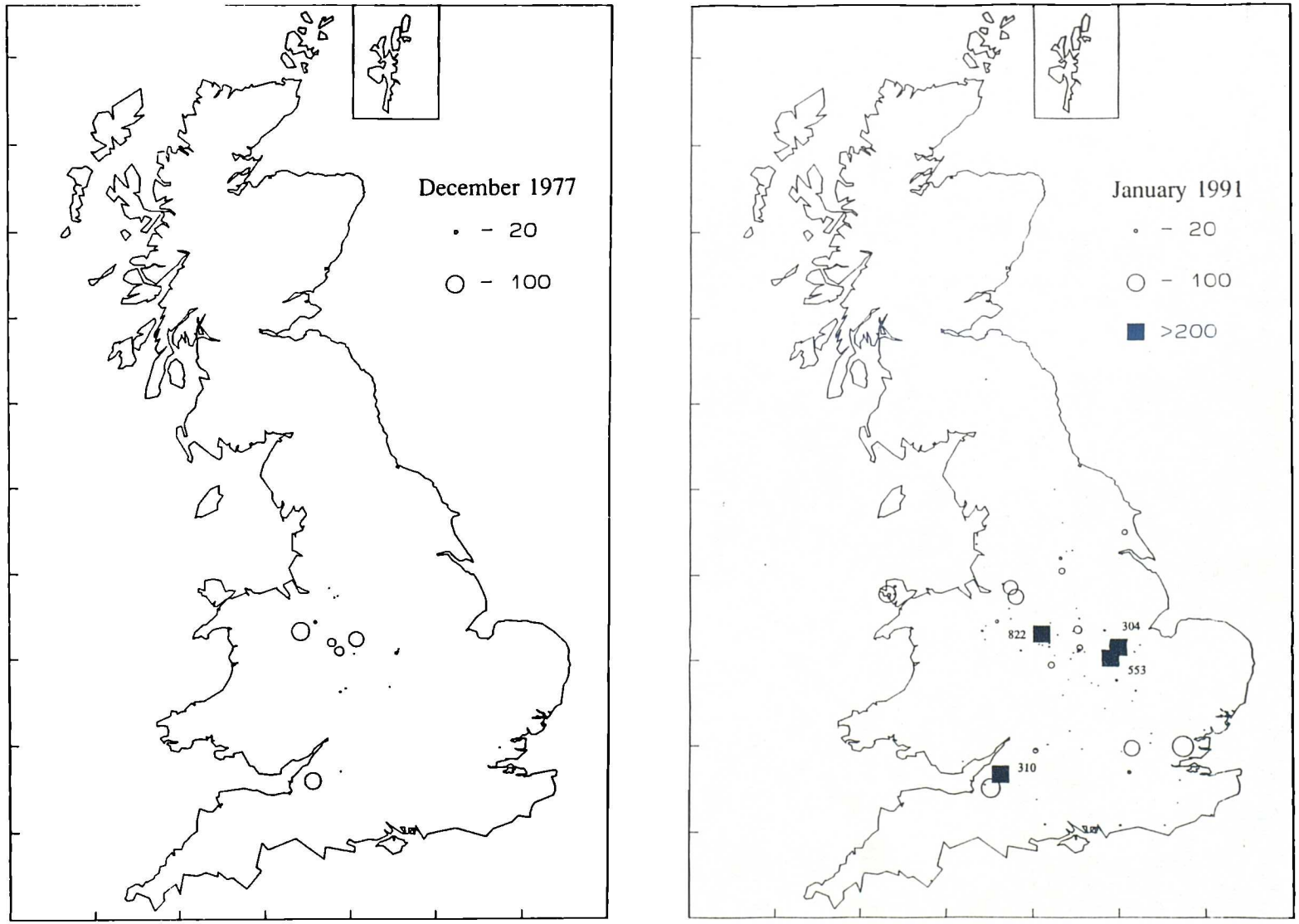

FIGURE 1.1. Distribution of Ruddy Ducks in Great Britain in December 1977 and January 1991 (data from National Waterfowl Counts).

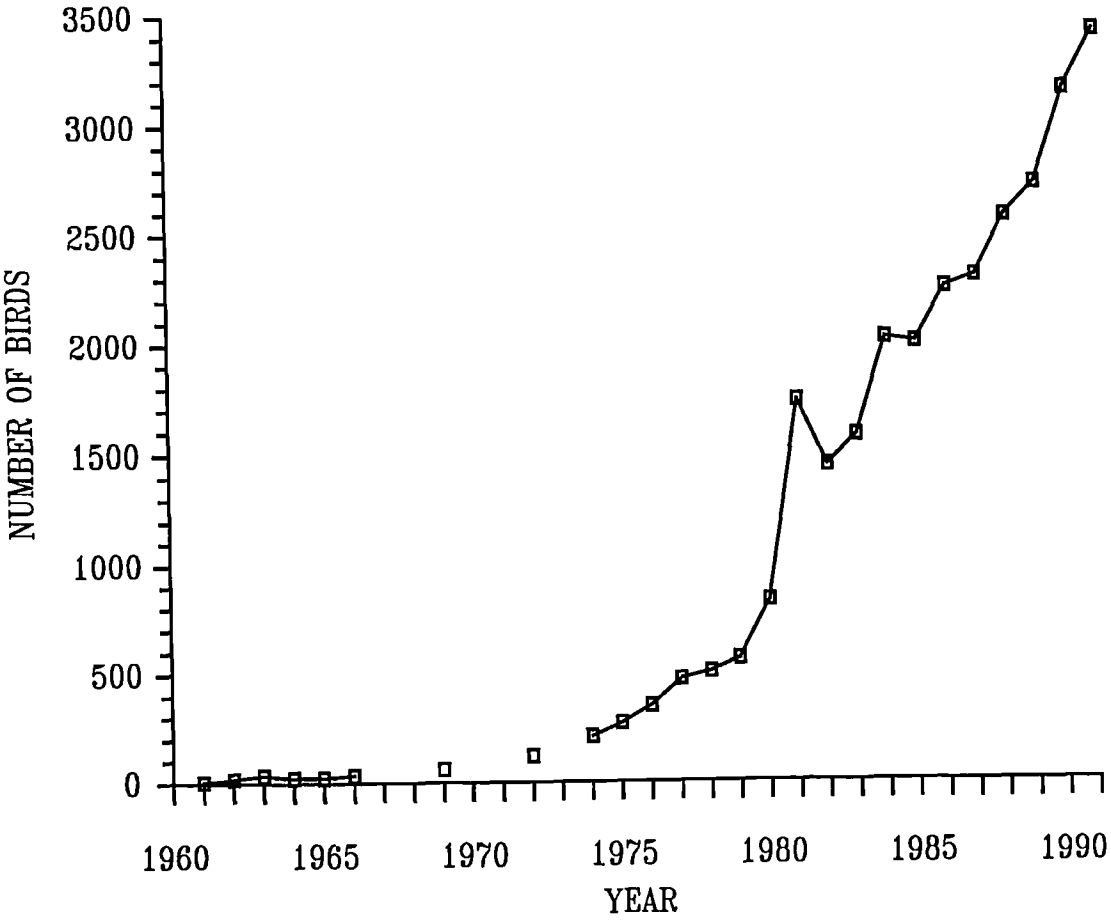

FIGURE 1.2. Annual maximum monthly count of Ruddy Ducks in Great Britain from winter 1960/61 to winter 1990/91 (data from National Waterfowl Counts).

2. The mortality was real and Ruddy Ducks were able to compensate for this natural winter mortality.
3. The mortality figure was an artefact caused by a relatively lower February count due to the Ruddy Duck's habit of dispersing to moult or begin breeding from February onwards.

There have been declines of between 0.01% and 46.2% (mean = 15.9%) between the December and February NWC totals in 11 of the last 16 years, while there have been declines in the maximum monthly count in subsequent years in only two. This could suggest that dispersal is the major factor in the December-February declines. The two declines in subsequent years may be explained by direct cold weather mortality or by cold weather dispersal as observed in 1978/79 (Vinicombe and Chandler 1982). The maximum monthly counts in the two hard winters which show declines from previous winters were made in November, before the periods of cold weather and before maximum monthly counts usually occur. Therefore, the low counts after the cold periods may be due to cold weather dispersal combined with a limited count coverage.

Although captive stifftails are known to be susceptible to cold weather mortality (N.S. Jarrett pers. comm.), the British population of Ruddy Ducks does not appear to be significantly affected by hard winters (Table 1.1). This is supported by the fact that the number of Ruddy Ducks in Great Britain actually increased in winters following the hard winters of 1978/79, 1984/85, 1985/86 and 1986/87. However, the hard winter of 1981/82 may have caused significant mortality as the Ruddy Duck population did not recover to the previous years total until the winter of 1983/84.

Assuming a 90% count efficiency for Ruddy Ducks counted during NWC (Owen *et al* 1986), the latest population estimate for Ruddy Ducks in Great Britain is 3427 birds in January 1991 (from Kirby *et al* 1991), an increase of two orders of magnitude since first breeding in 1960. Four sites in January 1991 held in excess of 200 birds: 822 at Blithfield Reservoir, 553 at Rutland Water, 310 at CVL and 304 at Eyebrook Reservoir, Leicestershire (Fig. 1.1).

It has been generally understood that the feral British population of Ruddy Ducks arose solely from Slimbridge escapees and their progeny, yet there was one deliberate release

by The Wildfowl Trust, of three or four females onto CVL in 1961 (Hudson 1976; Lever 1977). Hudson (1976) and Lever (1977) argue that this deliberate release had no discernible effect on the development of a feral population in Great Britain as feral breeding had already occurred at CVL and the number of breeding birds at CVL remained at one or two pairs until the 1970s. This may not be true as the released birds may have been involved in those breeding attempts. Firstly, the original breeding female may have died and been replaced by one of the released birds and, secondly, the second pair may have included one of the released birds whose young dispersed to areas away from CVL to breed. There has been at least one other documented deliberate release and probably many other undocumented cases. Eight birds were released at Blunham Lake, Bedfordshire in 1981 (Smith 1986).

Although Ruddy Ducks have been extensively studied in their native North America, especially during the breeding season (e.g. Joyner 1975; Gray 1980), work in Great Britain has been limited, mainly as a result of their relatively recent introduction. Hudson (1976) provided a fairly detailed account of their introduction and population increase up to 1976 while Vinicombe and Chandler (1982) described cold weather movements (see above). Ladhams (1977) provided a general description of the breeding behaviour of birds at CVL and Carbonell (1983) studied the breeding biology of captive birds at WWT's centre at Slimbridge. Apart from a progress report on this study (Hughes 1990), further knowledge is limited to records in county bird reports and the documentation of first breeding records (e.g. Smith 1986).

The overall rationale of this project was to determine what interactions, if any, occur between introduced Ruddy Ducks and native British species of bird through a detailed study of their behaviour throughout the year. Details of social interactions were recorded during time budgets collected during the winter, courtship and brood-rearing periods. Chapter 2 describes the diurnal and nocturnal activity of Ruddy Ducks at CVL and investigates the effect of time of day, date and weather on their behaviour. The diurnal and nocturnal diving behaviour is also examined in detail. Differential behavioural investment and diving ability depending on age and sex is assessed. Chapter 3 provides a description of the behaviour of courting male Ruddy Ducks at Mere Sands Wood Nature Reserve (MSWNR), Lancashire and considers differential behavioural investment in terms of pairing status, time of day, date, temperature and the presence/absence of other Ruddy

Ducks. The activity of brood female Ruddy Ducks at MSWNR and the change in their behaviour with time of day, temperature and brood age is assessed in Chapter 4.

Social interactions recorded during the winter, male courtship and brood female time budgets are considered in Chapter 5, including an evaluation of the change in the number, duration and intensity of interactions recorded in relation to time of day and date/pairing status in courting males and time of day and brood age in brood females. The rate of intra- and interspecific interaction is then evaluated and compared with that observed in other waterbirds before an assessment of the present and potential effect of interspecific interaction on native waterbirds. Finally, the effect of the introduction of the Ruddy Duck into Great Britain is discussed on a national and international level in Chapter 6.

CHAPTER TWO.

TIME BUDGETS AND DIVING BEHAVIOUR OF RUDDY DUCKS WINTERING AT CHEW VALLEY LAKE, AVON.

2.1 INTRODUCTION

Until recently, there had been only limited research into the feeding ecology of diving ducks during the non-breeding season since the early work of Klíma (1966), Nilsson (1969a, 1969b, 1970a, 1970b, 1970c, 1972, 1974) and Willi (1970). Most emphasis has been placed on dabbling ducks and this is perhaps not surprising, as the economic importance of dabbling duck populations has long been recognised. Diurnal time budgets have now been compiled for the majority of northern hemisphere dabbling ducks and their importance and implications for applied aspects of species and reserve management have been realised (eg. Paulus 1984, 1988a, 1988b). In recent years, more effort has been channelled into the study of winter aggregations of diving ducks. These include not only time budgets (Pedroli 1982; Hohman and Rave 1990), but also studies of aggression, habitat segregation and social hierarchies (Alexander and Hair 1979; Alexander 1980; Bergan 1986; Bergan and Smith 1989).

Some studies of wintering anatids have related activity budgets to the amount of disturbance present at a site (Nilsson 1970b; Pedroli 1982; Paulus 1984) and many studies have attempted to describe the effect of climatic variables on behaviour (eg. Paulus 1984, 1988a, 1988b; Quinlan and Baldasarre 1984; Miller 1985; Bergan 1986; Morton *et al* 1989), albeit with little success. Most, if not all, winter time budget studies attempt to describe changes in behaviour as the season progresses (see Paulus 1988b for review). However, it is well known that there are many factors affecting the differential behavioural investments of waterfowl within and between species.

Although it is widely known among waterfowl biologists that information relating to the nocturnal behaviour of waterfowl is crucial to the understanding of their wintering ecology (Jorde and Owen 1988; Paulus 1988b), there have been few studies which have adequately sampled the nocturnal period (Pedroli 1982; Paulus 1984; 1988a; Bergan 1986; Bergan *et al* 1989).

Paulus (1988b) provided a comprehensive review of the time budgets of non-breeding

Anatidae whilst reviews of nocturnal activity budgets and nocturnal feeding were presented in Jorde and Owen (1988) and Owen (1991) respectively. All three reviews included consideration of the many factors controlling differential behavioural investment.

I studied the diurnal and nocturnal behaviour and the feeding ecology of Ruddy Ducks wintering in Avon and attempted to investigate changes in behavioural investment with time of day, date and fluctuations with certain climatic variables.

2.2 STUDY AREA

Both diurnal and nocturnal time budgets were collected at Chew Valley Lake (CVL), Avon (Figures 2.1 and 2.2), one of the main wintering sites for Ruddy Ducks in Great Britain. CVL lies approximately 10km south of Bristol (51° 19'N, 2° 37'W) and was built by Bristol Waterworks Company (now Bristol Water Company) as a drinking water reservoir to meet the increasing demands of the Bristol conurbation. Construction work began in 1950 and flooding was complete by April 1956 (Williams 1973). At its maximum capacity, the lake has a surface area of 494ha, a shoreline of 15.4km and a capacity of 29,000,000m^3. The catchment area of the lake covers 5130ha. Much of this consists of triassic Keuper Marl clay, however, it also includes the carboniferous limestone areas of the northern slopes of the Mendip Hills (Wilson *et al* 1971). The main inflow is provided by the River Chew which flows into Herriot's Pool at the southern end of the lake (Fig. 2.2). CVL is shallow, considering its size, with an average water depth of only 4.27m and a maximum depth of 11.28m.

Wilson *et al* (1971) found CVL to be one of the most eutrophic lakes in Great Britain with a restricted diversity of invertebrates. The main benthic organisms were chironomids and oligochaetes, which were present at densities of 2800/m^2 and 2100/m^2 respectively. Hilton (1990) found the faunal diversity and the main families of invertebrates in the lake to be similar to that found by Wilson *et al*. The absence of the expected diversification of the invertebrate fauna as the lake matured is probably caused by a combination of factors. Firstly, the high turbidity of the lake, caused by wind action, will limit the growth of submerged macrophytes and hence restrict the development of the invertebrate fauna. Secondly, the regular seasonal fluctuations in the water level will restrict the littoral fauna, especially when the drawdown is as extensive as in recent years. During

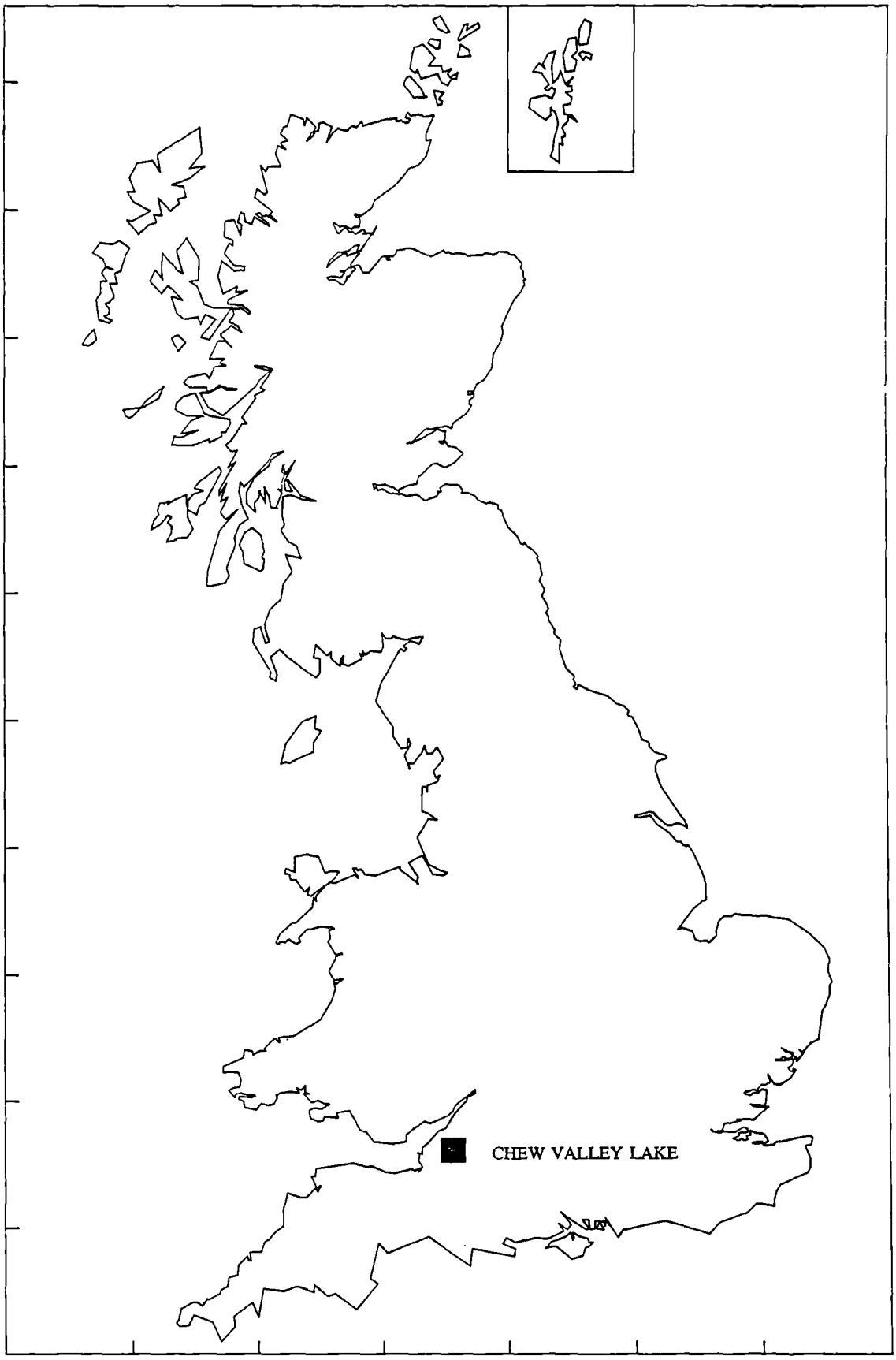

FIGURE 2.1. Location of CVL.

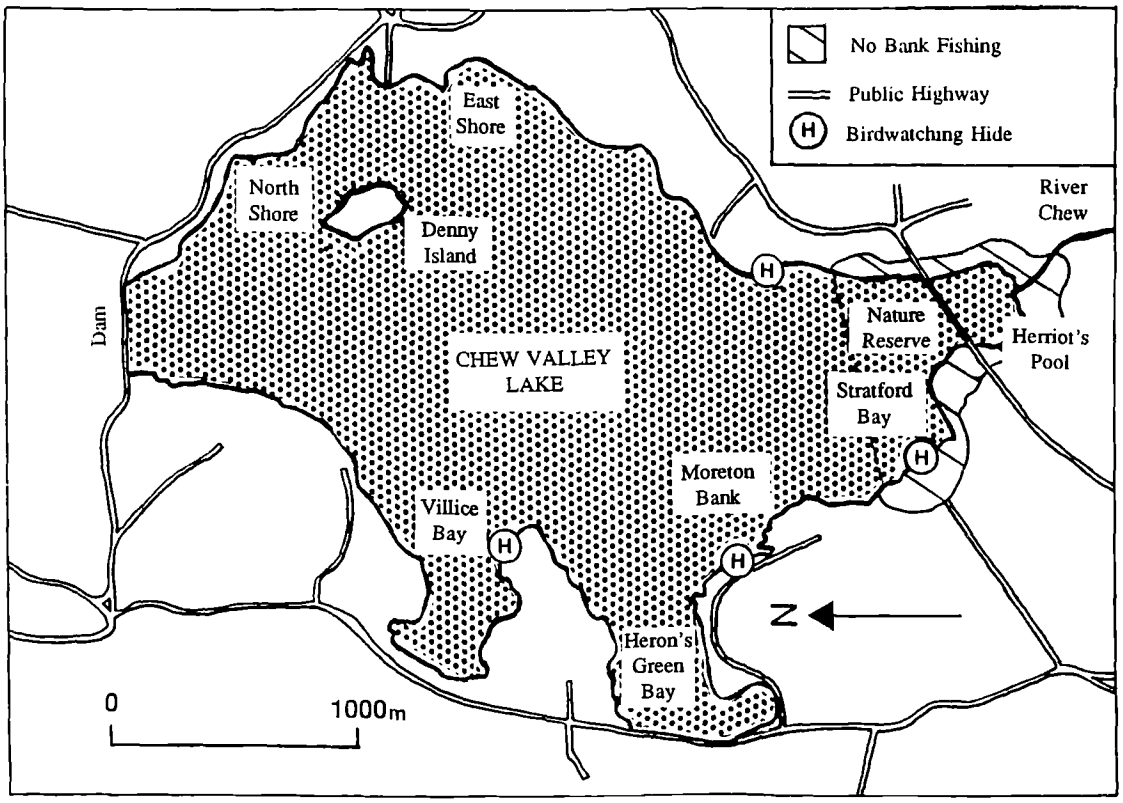

FIGURE 2.2. Detailed map of CVL.

1989 and 1990, the volume of water in the lake fell to 35% and 22% respectively, of its maximum capacity (B. Handford pers. comm.). The latter value represents the third lowest level the lake has reached in the 35 years since it was flooded.

Much of the eastern and southern shores of the lake are covered with well-established stands of Common Reed *Phragmites australis*, whereas the northern shores and the bays on the western shore lack this dominant lakeside vegetation. This is mainly due to erosion caused by wave action from the prevailing south-westerly wind. Amphibious Bistort *Polygonum amphibium*, Horse-radish *Armoracia rusticana* and Reed Canary Grass *Phalaris arundinacea* are the predominant emergent plants growing in shallow water where reedbeds have not become established (Avon Wildlife Consultants 1987). In years when water levels are low, exposed mud is rapidly colonised by a variety of annual weeds, such as Scentless Mayweed *Matricaria perforata* and Marsh Cudweed *Filaginella uliginosa*.

The lake is managed as a trout fishery by Bristol Water Company and is stocked each year with Brown Trout *Salmo trutta* and Rainbow Trout *Salmo gairdinerii*. Fishing on the lake is allowed from March to October each year, both from the bank and from motor launches. The southern end of the lake was designated as a nature reserve in 1969 and is now managed by Bristol Water Company, Avon Wildlife Trust and members of Chew Valley Ringing Station. The majority of wintering birds, including the main flock of Ruddy Ducks, congregate in this area during the day, however, there are reasonable concentrations elsewhere, notably in Heron's Green and Villice Bays and to the north-east of Denny Island (Fig. 2.2). Waterbirds use these sites in greater numbers when south-westerly gales create rough water conditions in the nature reserve. Under such conditions, Ruddy Ducks are also found sheltering in the lee of Moreton Bank. Bristol Water Company have provided a number of birdwatching hides to complement the natural observation sites around the lake.

During the winter, CVL may hold up to one third of the British population of Ruddy Ducks and is internationally important for Gadwall *Anas strepera* and Shoveler *A. clypeata*. The lake regularly holds nationally important numbers of Little Grebe *Tachybaptus ruficollis*, Great-crested Grebe *Podiceps cristatus*, Teal *Anas crecca crecca*, Pochard *Aythya ferina*, Tufted Duck *A. fuligula* and Goosander *Mergus merganser*. In

1985, CVL was designated a Site of Special Scientific Interest by the Nature Conservancy Council and as a Special Protection Area under the EC Bird Directive (1979).

Since Ruddy Ducks first occurred at CVL in 1957, there has been a regular winter gathering of birds. Numbers build up in autumn and peak in the first few months of the New Year (Fig. 2.3). Maximum counts at CVL may be associated with hard weather movements from more northerly sites in the country or, in less severe winters, with a spring moult concentration. The wintering flock at CVL regularly reaches 600+ with a maximum of 1064 birds counted in March 1987 (K. Vinicombe in litt.).

2.3 METHODS

2.3.1 Diurnal Time Budget

Diurnal time budget data were collected on the main flock of Ruddy Ducks at CVL from 20 January to 26 February 1988. All daylight hours, from 0800h until 1600h, were sampled twice in a unit of three days and the study period consisted of 11 time units or 33 study days. Observations were made from Stratford Bay Hide (Fig. 2.2) using a 20 (wide-angle) x 60 Kowa telescope and 10 x 50 Carl Zeiss Jena Jenoptem binoculars.

Three age/sex categories were recognised: adult males in alternate (or breeding) plumage, adult males in basic (or non-breeding) plumage and females/juveniles. To avoid the ambiguity of plumage nomenclature, all plumage terminology follows Humphrey and Parkes (1959). These terms describe the plumage of the bird rather than the season or the state of the breeding cycle which may be confusing. The terms "summer" and "winter" plumage are especially unsuitable when applied to the Anatidae. For example, Garganey *Anas querquedula* or Shoveler may not fully acquire their alternate plumage until springtime, whereas most Mallard *A. platyrhynchos* will have completed their pre-alternate moult by the end of autumn.

Ruddy Ducks show a different strategy of moult to other species of ducks in the northern hemisphere. Most anatids attain their alternate plumage in early winter and retain it until the onset of breeding, from which point they begin to moult into their basic, or eclipse plumage. Although the Ruddy Duck still acquires the same feather generations as other ducks, the timing of the moult differs. Ruddy Ducks acquire their alternate plumage in

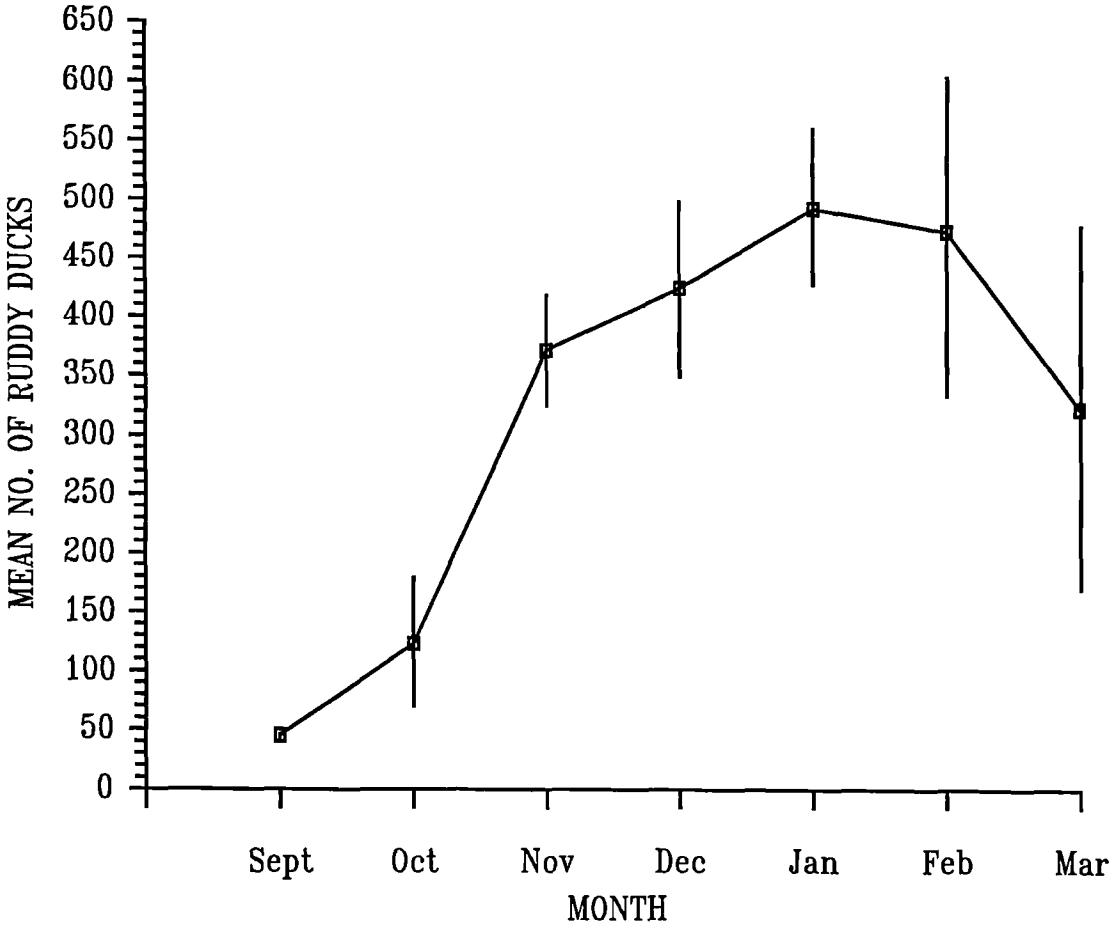

FIGURE 2.3. Mean monthly numbers of Ruddy Duck wintering at CVL, 1985/86-1989/90 (five year means from National Waterfowl Counts). Vertical bars represent ± 1 S.E..

late winter/early spring and retain it until late summer when breeding is complete. They then moult into their dull basic plumage which they wear until the following spring. Most British Ruddy Ducks exhibit this pattern of moult, but some birds, usually males, may attain their alternate plumage as early as January. It is quite common to see males in full alternate plumage in the wintering flock at CVL.

From hereon, males in alternate plumage will be referred to as "alternate males" and males in basic plumage as "basic males". Although females and juvenile birds of both sexes could be accurately separated with reasonable views, this was not possible with more distant observations and for this reason no distinction was made between these two categories.

Female/juvenile birds and adult males were observed alternately as were basic males and alternate males. Using this selection procedure, each bird was then chosen randomly from the wintering flock and its behaviour recorded continually for 30 minutes before switching to the next bird. Birds usually surfaced within four metres of their point of submergence and the use of a wide-angle lens on the telescope reduced the number of focal individuals lost while diving. An electronic event recorder, which recorded activity at 0.2s intervals, was used to collect the activity budget data.

Ambient temperature was recorded at the beginning of every observation period, whereas other climatic variables, such as mean wind speed (measured on the Beaufort Scale), were recorded daily. Any major climatic changes during the observation periods were also recorded. Sex-ratio counts of the flock under observation were made on 22 days during the study. Note that the female category may include some misidentified juvenile males from more distant observations.

Thirty three behaviours were identified and combined into nine mutually exclusive behaviour categories for analysis (Table 2.1).

REST - Sleeping and pseudo-sleeping behaviour (cf. Cornwall and Bartonek 1963), that is, the head-on-back posture which is typical of resting anatids.

TABLE 2.1. Summary of behaviours exhibited by Ruddy Duck wintering on CVL.

REST	- Sleep - Pseudosleep

COMFORT MOVEMENTS	- Preen
	- Roll-cheeks-on-back
	- Rest-preen
	  - Foot-shake
	  - Tail-shake
	- Scratch
	- Stretch
	- Bill-dip
	- Bathe
	- Wing-shiver
	- Wing-flap
	- Minor comfort activities
	  - Yawn
	  - Foot-shake
	  - Tail-shake
	  - Head-shake

SWIM	- Loaf - Locomotion - Inter-dive interval
ALERT	- Head-up - Extreme head-up - Extreme head-up-tail-up
FEED	- Dive - Dabble - Drink
FLY	
SKEETER	

SOCIAL INTERACTION	- Intraspecific
	  - initiated by study bird
	  - initiated by another bird
	- Interspecific
	  - initiated by study bird
	  - initiated by other species
	  - Avoidance

COURTSHIP	- Bubbling display

COMFORT MOVEMENTS - Self-maintenance activities relating to plumage care and general comfort. This category includes the following behaviours:-

Preen - Plumage maintenance. Includes a type of preening which may be peculiar

to stifftails, in which the birds rear up vertically in the water and preen their bellies. Most other waterfowl roll on their sides in the water to carry out this act.

Rolling-cheeks-on-back - Common behaviour in the sequence of feather-care, in which the head and cheeks are rolled on the upper mantle. A ritualised version of this behaviour is included in the male Ruddy Duck's courtship display.

Rest-preen - Comfort movements performed while in the pseudo-sleeping posture. Two common examples of this type of behaviour are foot-shaking and tail-shaking although both may also be performed while not in the pseudo-sleeping posture.

Scratch - Use of the feet to scratch any part of the body.

Stretch - Any stretching movement. The most common stretching movement involves the Ruddy Duck simultaneously stretching both wing and leg from the same side of its body.

Bill-Dip - Placing the bill in the water before shaking it from side to side. In this context, this behaviour is involved with plumage maintenance, however, there is a more exaggerated and ritualised version of bill-dipping which is included in the male Ruddy Duck's repertoire of courtship behaviour.

Bathe - Washing activity.

Wing-shiver (Wing Quivering of Ladhams (1977)) - An activity which appears to be peculiar to stifftails, in which the wings are "shivered" while in the folded position. Siegfried (1973a) suggested that this behaviour has a thermogenesis function, although in some instances it appears to be a simple comfort movement.

Wing-flap - Intensive and continuous wing-flapping, often for more than ten seconds. Usually occurs at the end of preening bouts and may also serve as a method of thermogenesis.

Other less common comfort movements, such as yawning and foot-, tail- and

head-shaking, are also included in the comfort movements behaviour category. For a more comprehensive description of comfort movements in ducks see McKinney (1965) and Alexander (1980).

SWIM - This category includes locomotion, loafing behaviour and the inter-dive interval. The use of the event recorder necessitated the inclusion of this rather broad category as it was impossible to immediately identify a swim-related behaviour. For example, "swim" includes the inter-dive interval of feeding activity because it was not possible to determine whether a bird would dive again after surfacing.

ALERT - Head-up, extreme head-up and extreme head-up-tail-up behaviour (in which the tail is raised to an angle of 90° or more to the surface of the water). Extreme-head-up-tail-up behaviour was typical of the posture assumed when under attack from Black-headed *Larus ridibundus* or Common Gulls *L. canus* which dive-bombed the Ruddy Ducks while flying in to roost on the lake.

FEED - Diving, dabbling and drinking activity.

FLY.

"SKEETER" - This behaviour always precedes flying but does not always lead to flight. If Ruddy Ducks are disturbed, but there is no immediate danger, they will often run across the surface of the water, flapping their wings while not actually taking off. Communal "skeetering" sometimes occurs, in which many birds patter across the water surface seemingly without stimulus, an activity that Cramp and Simmons (1977) referred to as "patter rushing".

SOCIAL INTERACTION - Intra- and interspecific aggression and other inter-bird associations. Includes the category "avoidance" in which a Ruddy Duck dives or makes a manoeuvre to escape another bird which is oblivious to the actions of the Ruddy Duck. Additional details concerning social interactions were recorded including the species involved, the initiator of the interaction, details relating to the intensity of the interaction and the final outcome. Social interactions are analysed in detail in Chapter Five and will not be considered further here.

2.3.2 Nocturnal Time Budget

Nocturnal time budget data were collected at CVL between 30 January and 7 March 1990. All hours of darkness, from 1800h until 0600h, were sampled twice in a unit of two days and the study period consisted of 14 time units or 28 study days. Observations had to be cancelled on three other days when weather conditions were unsuitable. Observations were made at Heron's Green Bay on the western shore of the lake (Fig. 2.2) using a 'Bostrok Nightkeeper' night-viewing unit fitted with a 150mm fixed focus mirror-lens (f 1.0).

Males and females/juveniles could be identified, however, it was not possible to age the birds or determine their plumage category. Birds were selected for observation in a similar manner to that used during the diurnal time budget. Each bird was observed continuously for 30 minutes and the behaviour recorded using the event recorder. Males and females/juveniles were observed alternately when possible, but due to the excess of males in the wintering flock and the limited scope of the night-viewing equipment this was not always possible.

Climatic variables were recorded at the start of every observation period. These included ambient temperature, wind speed (measured on the Beaufort Scale), the presence/absence of precipitation, the extent of cloud cover (on a scale of one to eight) and moon visibility (visible or absent/obscured).

The behaviour categories recognised in the nocturnal budget were similar to those described for the diurnal work (Table 2.1) though subtle behavioural changes, such as between rest and rest-preen, could not be detected.

2.3.3 Data Analysis

The number of records of each behaviour were expressed as a percentage of the total records for each observation period and any mutually exclusive behaviour category which constituted $\geq 5\%$ of the total time budget was defined as a major behaviour and selected for further analysis. No analyses were performed on behaviour categories which constituted $<5\%$ of the total time budget.

The data were analysed using the SYSTAT computer package (Wilkinson 1987). Data when birds were out of sight and observation periods less than ten minutes long were excluded from the analysis. Date was represented in the analysis by days from the start of the study period. All means stated in this chapter are followed by the standard errors of the means in parenthesis. All statistical tests were deemed to be significant below the 0.05 two-tailed probability level ($2\alpha<0.05$). Sample sizes in these tests refer to the number of individual observation periods and therefore represent the maximum number of birds observed.

Where appropriate, figures are plotted with error bars of one standard error and annotated with sample sizes relating to individual data points.

The Lower Critical Temperature (LCT) for Ruddy Ducks was calculated using the Aschoff-Pohl equation. Body mass data were obtained from wild Ruddy Ducks caught between 1979 and 1989 at The Wildfowl & Wetlands Trust's ringing station at Abberton Reservoir, Essex. Birds in their first calender year of life were excluded from the analysis as all birds at CVL during the time budget study periods (January to March) were in their second calender year or above. Due to a low sample size, all other age/sex classes caught at all times of the year were included and amalgamated.

To investigate the effect of temperature on the birds' behaviour, the data were separated into three groups:-

1. Below median ambient temperature.
2. At median ambient temperature.
3. Above median ambient temperature.

As previously stated in section 2.3.2, the nocturnal time budget data were collected in Heron's Green Bay on the western shore of the lake (Fig. 2.2). The effective range of the night viewer was approximately 100m. This allowed observations to be made in the inner section of the bay only, however, birds sometimes swam out of the bay during observation and could be followed outside the effective range of the night-viewer. Extensive periods of swimming behaviour resulted at the end of such observation periods. These extensive periods of swim were removed from the analysis as it was not possible to distinguish

other behaviours, such as comfort movements, at these distances. This effectively means that the nocturnal time budget refers only to the behaviour of Ruddy Ducks in the inner section of the bay.

Two separate analyses were performed to investigate the effect of wind on the Ruddy Ducks' nocturnal behaviour. Firstly, an analysis of the direct effect of wind using two wind speed categories: ≤ force 4 and ≥ force 5. Secondly, an analysis of the possible longer term effect of strong wind on their behaviour using three categories to describe the wind conditions on a nightly basis:-

1. Actual wind speed ≤ force 4, maximum nightly wind speed ≤ force 4.
2. Actual wind speed ≤ force 4, maximum nightly wind speed ≥ force 5.
3. Actual wind speed ≥ force 5, maximum nightly wind speed ≥ force 5.

Five variables concerning the lunar cycle were also included in the analysis. The direct effect of the lunar influence was investigated by recording the extent of cloud cover (on a scale of one to eight) and moon visibility (visible or absent/obscured), whereas moon phase, days since last full moon and days since last new moon were included to examine the indirect effect of the lunar cycle. The variable "time of night", that is, hours from 1800h, was used to investigate change of behaviour as the night progressed.

2.3.4 Dive Time Analysis

Original behavioural sequences produced by the event recorder were reanalysed to extract information on dive lengths and the associated inter-dive intervals. The first and last dives in these dive/inter-dive sequences were discounted then a feeding bout was defined as a sequence of five or more dive cycles, that is, combinations of dive times and inter-dive intervals. Any dive sequences falling below this cut-off point were not included in the analysis. Similarly, dives made for any purpose other than feeding, for example, avoidance dives or short dives which occurred during preening, were not included. A feeding bout was assumed to have ended either when a behaviour other than dive or swim occurred or when the duration of swimming following a dive exceeded 40 seconds. Depth readings were taken at nocturnal and diurnal Ruddy Duck feeding sites.

The Statistical Analysis System (SAS) package (Version 6) was used to analyse the data. Simple non-parametric correlations were used to examine the relationship between dive lengths and the associated inter-dive intervals and between those two variables and feeding bout number, time of day, date and ambient temperature. Three separate analyses were performed to investigate these relationships using original dive and inter-dive durations, mean durations per feeding bout and mean durations per bird (see section 2.3.5).

Dive frequency per feeding bout and per bird were also examined along with the number of feeding bouts per bird. For completeness, dive frequencies were also expressed as intensities, that is, dives per minute. As there are the same number of dives and inter-dives in each feeding bout, the terms "dive frequency" and "dive intensity" equally apply to the frequency and intensity of inter-dives.

In plots of dive time against inter-dive interval, data points with less than ten observations were excluded from the analysis.

2.3.5 Pseudoreplication

Pseudoreplication is defined as "the testing for treatment effects with an error term inappropriate to the hypothesis being considered" (Hurlbert 1984). In behavioural ecology, this often results from inferential statistics being used to test for treatment effects in experiments where treatments are not replicated (though samples may be) or where replicates are not statistically independent. This has often been the case in the analysis of dive time data. For example, when testing for differences in dive times between male and female waterbirds, some authors (*e.g.* Lovvorn 1990) have used the number of individual dive times as the experimental unit when the appropriate unit is actually the mean dive time per bird.

In this thesis, especially in the analysis of diving behaviour, results are presented both with pseudoreplication (which allows direct comparison with earlier studies) and without. However, future studies should strive to eliminate pseudoreplication from similar analyses.

2.4 RESULTS

2.4.1 Diurnal Time Budget

2.4.1.1 Diurnal Behaviour

The mean size of the main wintering flock of Ruddy Ducks under observation was 241.6 (± 27.79, range 49-489; Table 2.2). However, the National Wildfowl Counts showed a maximum winter count for the whole lake of 610 on 20 February 1988 (Fig. 2.4). The mean sex-ratio (males:females) of Ruddy Ducks at CVL during the study was 1.37 (± 0.075) with a range of 0.85-2.31 (Table 2.2, Fig. 2.5). In other words, the mean flock composition was 56.9% males and 43.1% females.

TABLE 2.2. Diurnal time budget - numbers of Ruddy Duck at CVL during the study period.

	N	Mean	S.E.	Max.	Min.
Number of males	22	136.2	16.07	279	30
Number of Females	22	105.5	12.31	216	19
Total numbers	22	241.6	27.79	489	49
% Males	22	56.9	1.29	69.8	46.0
% Females	22	43.1	1.29	54.0	30.2
Sex ratio (males:females)	22	1.37	0.075	2.31	0.85

The number of males in alternate plumage increased as the study period progressed. A count at the start of the study period on 23 January 1988 revealed that 18.8% (28/149) of the males in the wintering flock were in alternate plumage. This figure increased to approximately 50% at the end of the study although no accurate counts were made at that time. By 19 March 1988, 77.3% (109/141) of the males in the flock were in alternate plumage.

Non-parametric statistics were used for analysis, as examination of probability plots for the major behaviours showed that the time budget data were non-normally distributed even after angular transformation.

A total of 176 hours of observation produced 122.56 hours of usable data on a maximum

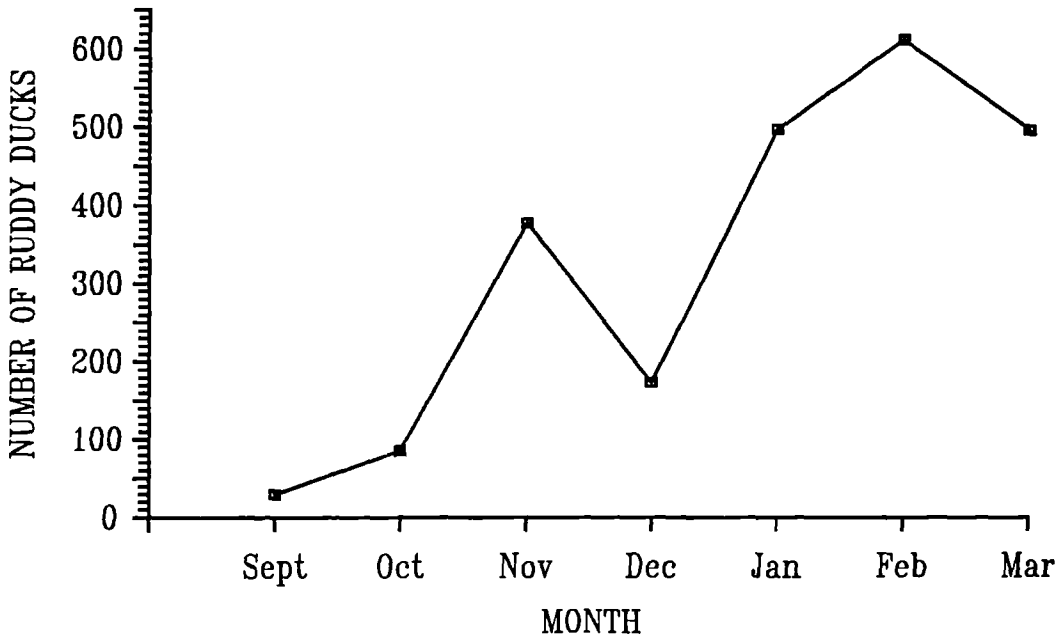

FIGURE 2.4. Numbers of Ruddy Duck at CVL during the winter of 1987/88 (data from National Waterfowl Counts).

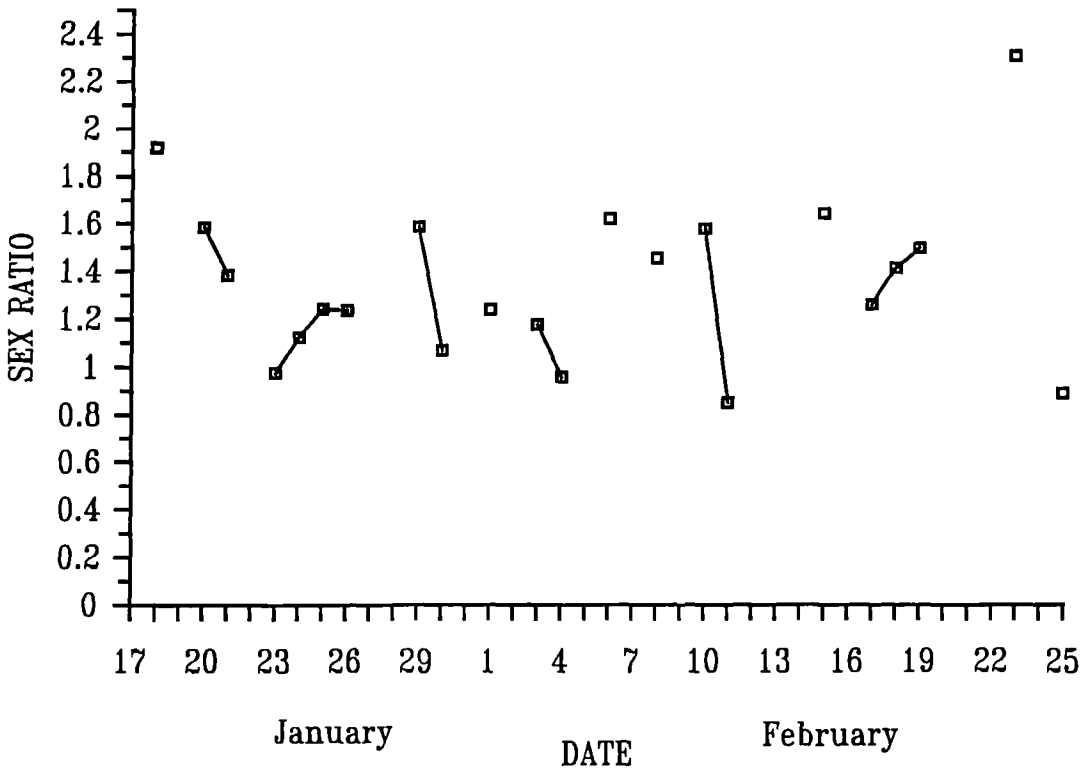

FIGURE 2.5. Sex-ratio of Ruddy Duck (males:females) in the main wintering flock at CVL during the winter of 1987/88 (lines join counts made on concurrent days).

of 280 birds (72 alternate males, 74 basic males and 134 females/juveniles). Alternate males, basic males and females/juveniles did not differ significantly in their four major behaviours (Kruskal-Wallis (KW) Tests, $p>0.05$; Table 2.3). Likewise, when both male categories were amalgamated there was no significant difference in behaviour between the sexes (Mann-Whitney (MW) U-Tests, $p>0.05$). All age/sex classes were therefore amalgamated for further analysis.

The Ruddy Ducks at CVL spent 70.26 (± 2.066)% of the daylight hours resting and only 6.82 (± 0.979)% actively feeding (Table 2.3). If the inter-dive interval is included in the latter value then the percentage time spent foraging increases to approximately 9.6%. Other major behaviours were comfort movements, which constituted 5.89 (± 0.551)% of the total time budget, and swimming, which made up 16.55 (± 1.310)% or approximately 13.8% excluding the inter-dive interval. Minor behaviour categories were alert, social interaction, fly and "skeeter".

2.4.1.2 Effect of Date on Behaviour

All of the major behaviours of the Ruddy Ducks wintering at CVL showed significant correlations with date. Resting was significantly positively correlated with date whilst swimming and feeding showed significant negative correlations (Table 2.4). However, a plot of mean daily behaviour against date revealed that it was not a simple linear relationship between the two variables (Figure 2.6). There was a marked change in behaviour between 1 February and 2 February. The amount of time spent resting was significantly greater after this point whilst there was significantly less feeding, swimming and comfort movements in the later part of the study period (MW U-Tests, $p<0.001$).

Not only was there an obvious change in behaviour on 2 February (Figure 2.6), there also appears to be a cyclical quality to the plots. This is especially true for the two main behaviours, swimming and resting. Examination of the lunar cycle for the study period showed that there was a full moon on 2 February and subsequent analysis revealed significant correlations between all of the dominant activities and days from the last full moon (Table 2.4). Comfort movements, swim and feed were significantly positively correlated with days since last full moon whilst rest was negatively correlated.

TABLE 2.3. Diurnal time budget (percent time in activity) of Ruddy Duck at CVL.

	Alternate Males		Basic Males		All Males		Females/ Juveniles		All Birds	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Major Behaviours										
Rest	71.02	4.208	68.94	3.949	69.97	2.875	70.59	2.983	70.26	2.066
Comfort Movements	5.42	1.067	5.81	0.815	5.62	0.667	6.18	0.895	5.89	0.551
Swim	16.17	2.507	16.97	2.398	16.57	1.728	16.53	1.993	16.55	1.310
Feed	7.12	1.948	7.84	1.983	7.48	1.386	6.10	1.382	6.82	0.979
Minor Behaviours										
Alert	0.22	0.063	0.32	0.080	0.27	0.051	0.50	0.090	0.38	0.051
Social Interaction	0.03	0.010	0.10	0.032	0	0	0.06	0.015	0.06	0.011
Fly	0	0	0.01	0.005	0.03	0.012	0.02	0.021	0.01	0.010
Skeeter	0.03	0.021	0.02	0.014	0.06	0.017	0.02	0.008	0.02	0.008
Number of Observation Periods	72		74		146		134		280	
Total Time Watched (Hrs)	31.50		32.26		63.76		58.8		122.56	

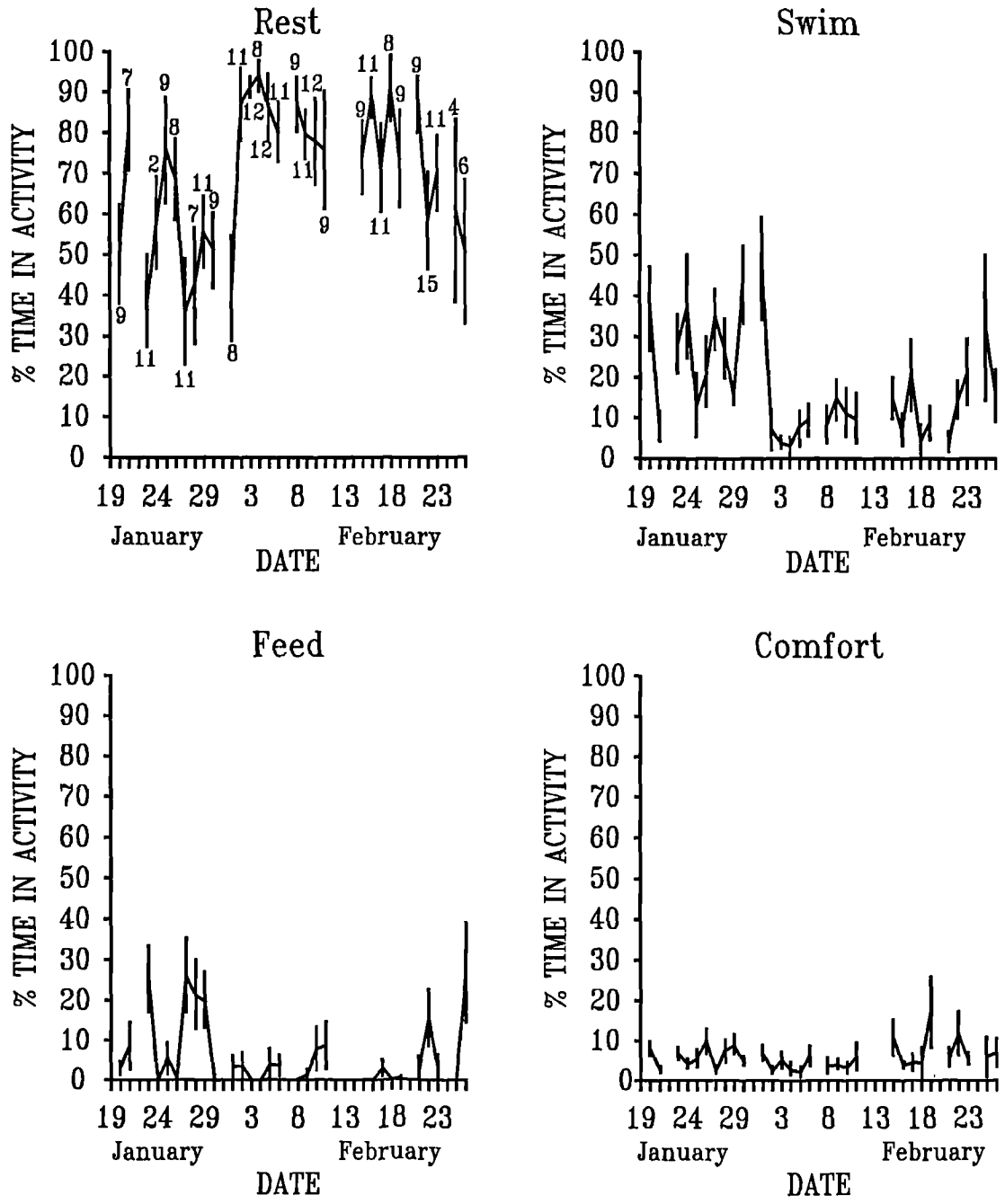

FIGURE 2.6. Change in diurnal activity of Ruddy Duck wintering at CVL with date. Vertical bars represent ± 1 S.E.. Sample sizes are given above error bars.

TABLE 2.4. Diurnal time budget of Ruddy Duck wintering at CVL - Spearman's correlation coefficients between major behaviours and date, ambient temperature, moon cycle and time of day. *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$.

	N	Date	Ambient Temperature	Daily Mean Temperature	Days From Last Full Moon	Time of Day
Rest	280	0.183 **	0.019	0.028	-0.301 ***	-0.032
Comfort Movements	280	-0.068	0.069	0.063	0.164 **	-0.009
Swim	280	-0.205 ***	-0.022	-0.034	0.294 ***	0.030
Feed	280	-0.253 ***	-0.056	-0.016	0.178 **	0.042

2.4.1.3 Effect of Time of Day on Behaviour

There were no significant correlations between the major behaviour categories and time of day (Spearman's correlations, $p>0.05$; Table 2.4). Similarly birds' behaviour did not differ between morning and afternoon (MW U-Tests, $p>0.05$). When behaviour was converted to mean half-hourly values and plotted against time of day, a decline in feeding activity was apparent around midday with an associated increase in resting (Fig. 2.7). Resting behaviour also declined sharply at 1600h when swimming increased markedly. Preening was highest in the early morning. Resting never fell below 50% of the half-hourly time budget, except for the value at 1600h. This value may be suspect due to a small sample size (N=3), but is probably genuine and caused by disturbance from gulls coming in to roost on the lake at this time.

2.4.1.4 Effect of Weather on Behaviour

The weather during the first three weeks of the study period was generally poor with overcast skies and frequent wind and rain. There was rain on seven of the 33 study days, all within the first two weeks and the wind speed reached force 5 on 12 days. Ten of these days were within the first three weeks of the study period and on two of them rough water conditions made observations impossible. The Ruddy Ducks at CVL spent significantly less time feeding in windy conditions (MW U-Test, $p<0.05$), but the time spent performing other behaviours was not significantly different from that in calmer conditions (Table 2.5). Only 4.73 (± 1.408)% of the daylight hours was spent feeding on days when the wind speed reached greater than force 4 on the Beaufort Scale, compared

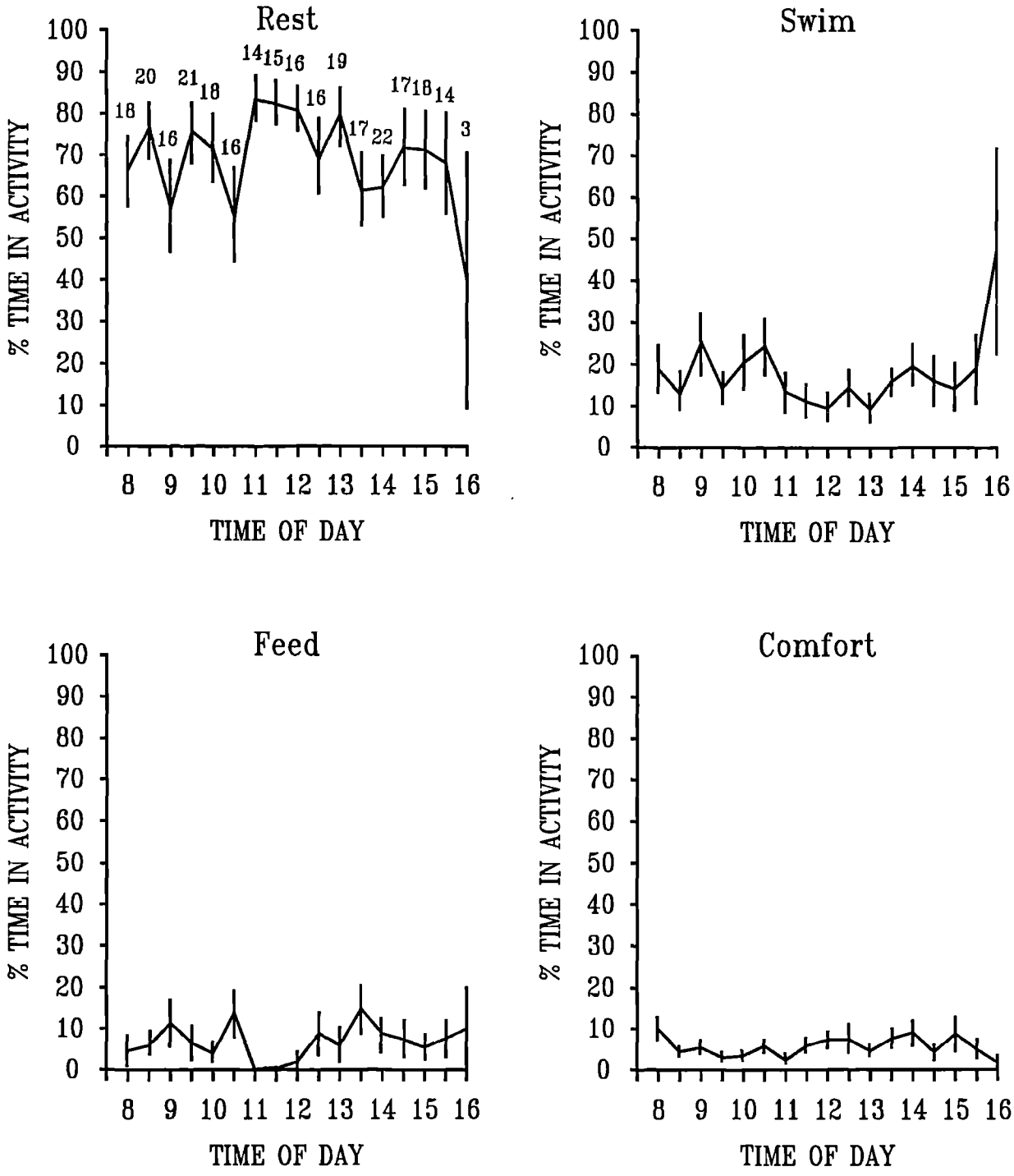

FIGURE 2.7. Change in diurnal activity of Ruddy Duck wintering at CVL with time of day. Vertical bars represent ± 1 S.E.. Sample sizes are given above error bars.

with 8.08 (± 1.312)% on days when the wind speed did not exceed force 4. On days when there were prolonged rain showers, the birds spent significantly more of their time feeding (MW U-Test, $p<0.001$).

TABLE 2.5. Diurnal time budget of Ruddy Duck wintering at CVL - effect of wind and rain on percent time spent in major behaviours. Means with different letters are significantly different (MW U-Tests, $p<0.05$).

	Mean Daily Wind Speed				Rain			
	≤ Force 4		≥ Force 5		Present		Absent	
	N=175		N=105		N=71		N=209	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Rest	68.50	2.664	73.21	3.259	63.04	4.647	72.71	2.256
Comfort Movements	6.80	0.816	4.36	0.530	4.48	0.658	6.37	0.701
Swim	16.12	1.566	17.27	2.330	17.69	2.429	16.17	1.551
Feed	8.08 a	1.312	4.73 b	1.408	14.37 a	2.655	4.26 b	0.889

The ambient temperature during the study period varied between -2 and 13°C with a median value of 5°C. The behaviour of the Ruddy Ducks at CVL did not show any significant change with change in ambient temperature. Assuming a body temperature of 40°C (after Owen and Dix 1986) and a mean body mass of 541.6 (± 8.28)g (N=114), the Lower Critical Temperature (LCT) for Ruddy Ducks was calculated as 13.1°C.

Ambient temperature and daily mean ambient temperature were not significantly correlated with any of the major behaviours (Table 2.4), but the amount of time spent preening did increase with increasing temperature (Fig. 2.8), albeit non-significantly. There were no significant differences in behaviour for the three temperature categories included in the analysis: below median ambient temperature, at median ambient temperature and above median ambient temperature (KW Tests, $p>0.05$).

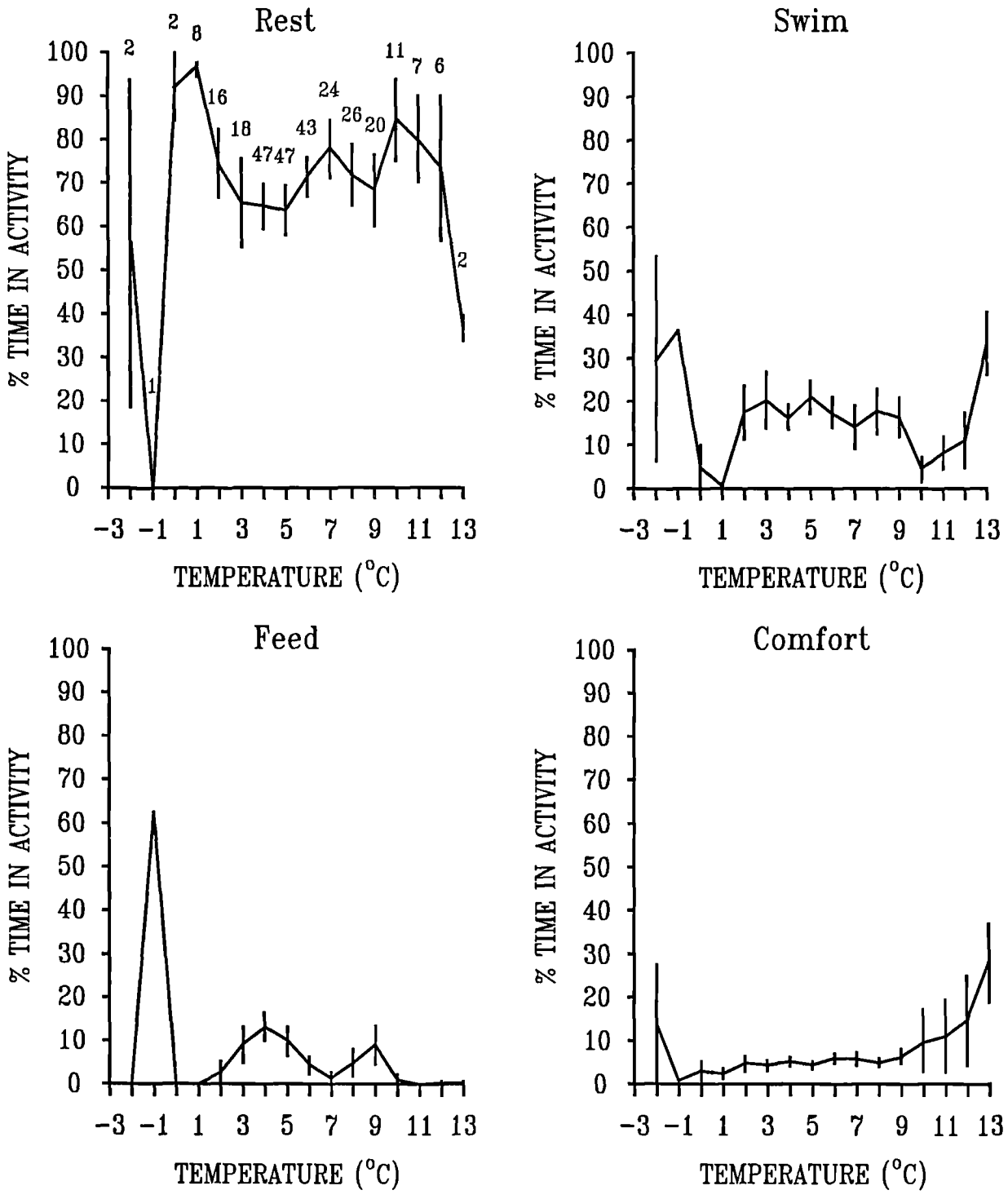

FIGURE 2.8. Change in diurnal activity of Ruddy Duck wintering at CVL with temperature. Vertical bars represent ± 1 S.E.. Sample sizes are given above error bars.

2.4.2 Nocturnal Time Budget

2.4.2.1 Nocturnal Behaviour

Non-parametric statistics were used for analysis as examination of probability plots for the major behaviours showed that the time budget data were non-normally distributed even after angular transformation.

Flocks of roosting Ruddy Ducks began to break up approximately one hour before sunset corresponding to the increased arrival of gulls which roost on the lake. A total of 186 hours of nocturnal observation produced 97.14 hours of usable data on a maximum of 236 birds (148 males and 88 females/juveniles). Table 2.6 summarises the nocturnal behaviour of Ruddy Ducks at CVL. Feeding and swimming made up the vast majority of the nocturnal time budget: 63.86 (± 1.124)% and 32.41 (± 0.625)% respectively in males and 68.91 (± 0.725)% and 30.83 (± 0.627)% respectively in females/juveniles. Females/juveniles spent significantly more time feeding than males (MW U-Test, $p<0.01$).

TABLE 2.6. Nocturnal time budget (percent time in activity) of Ruddy Duck wintering at CVL. Means with different letters are significantly different (MW U-Tests, $p<0.05$).

	Males		Females/Juveniles		All Birds	
	Mean	S.E.	Mean	S.E.	Mean	S.E.
Major Behaviours						
Swim	32.41	0.625	30.83	0.627	31.82	0.459
Feed	63.86 a	1.124	68.91 b	0.725	65.74	0.770
Minor Behaviours						
Rest	2.87	1.044	0.14	0.140	1.85	0.662
Comfort Movements	0.84	0.181	0.10	0.049	0.57	0.117
Alert	0.02	0.011	0.01	0.014	0.02	0.009
Social Interaction	0	0	0.01	0.006	0.01	0.002
Number of Observation Periods	148		88		236	
Total Time Watched (Hrs)	61.16		35.97		97.14	

If the inter-dive interval is included in the value calculated for feeding activity, the

percentage time spent foraging increases to 88.94% in males and 95.35% in females/juveniles. Minor behaviours were rest, comfort movements, alert and social interaction. Bubbling courtship display (see Chapter Three) was noted on one occasion, however, the duration of this activity was not sufficient for it to appear in the time budget.

2.4.2.2 Effect of Date on Behaviour

Date was not significantly correlated with either of the Ruddy Ducks' major behaviours (Table 2.7). A plot of mean nightly activity values against date (Fig. 2.9) showed that throughout the study period both sexes consistently spent 60-70% of the night feeding, although there was noticeably more variation in males. Males spent consistently less time feeding than females/juveniles throughout the study period.

TABLE 2.7. Nocturnal time budget of Ruddy Duck wintering at CVL - Spearman's correlation coefficients between major behaviours and date, ambient temperature, moon cycle and time of night. *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$.

	N	Date	Ambient Temp.	Daily Mean Temp.	Moon Phase	Days from last New Moon	Days from last Full Moon	Time of Night
Males								
Swim	148	0.037	0.099	0.159	-0.141	0.041	0.109	-0.050
Feed	148	-0.021	-0.084	-0.152	0.019	-0.076	-0.153	0.045
Females/juveniles								
Swim	88	0.178	-0.145	-0.102	0.014	-0.064	0.253 *	0.177
Feed	88	-0.176	0.139	0.095	-0.024	0.059	-0.257 *	-0.175

2.4.2.3 Effect of Time of Night on Behaviour

There were no significant correlations between the major behaviour categories and time of night (Spearman's correlations, $p>0.05$; Table 2.7). A plot of mean hourly behaviour values against time of night, showed that both males and females/juveniles consistently spent 60-70% of their time feeding throughout the night (Figure 2.10). Females/juveniles rested very little at all, whereas males showed a peak of resting between 2300 and 2400h.

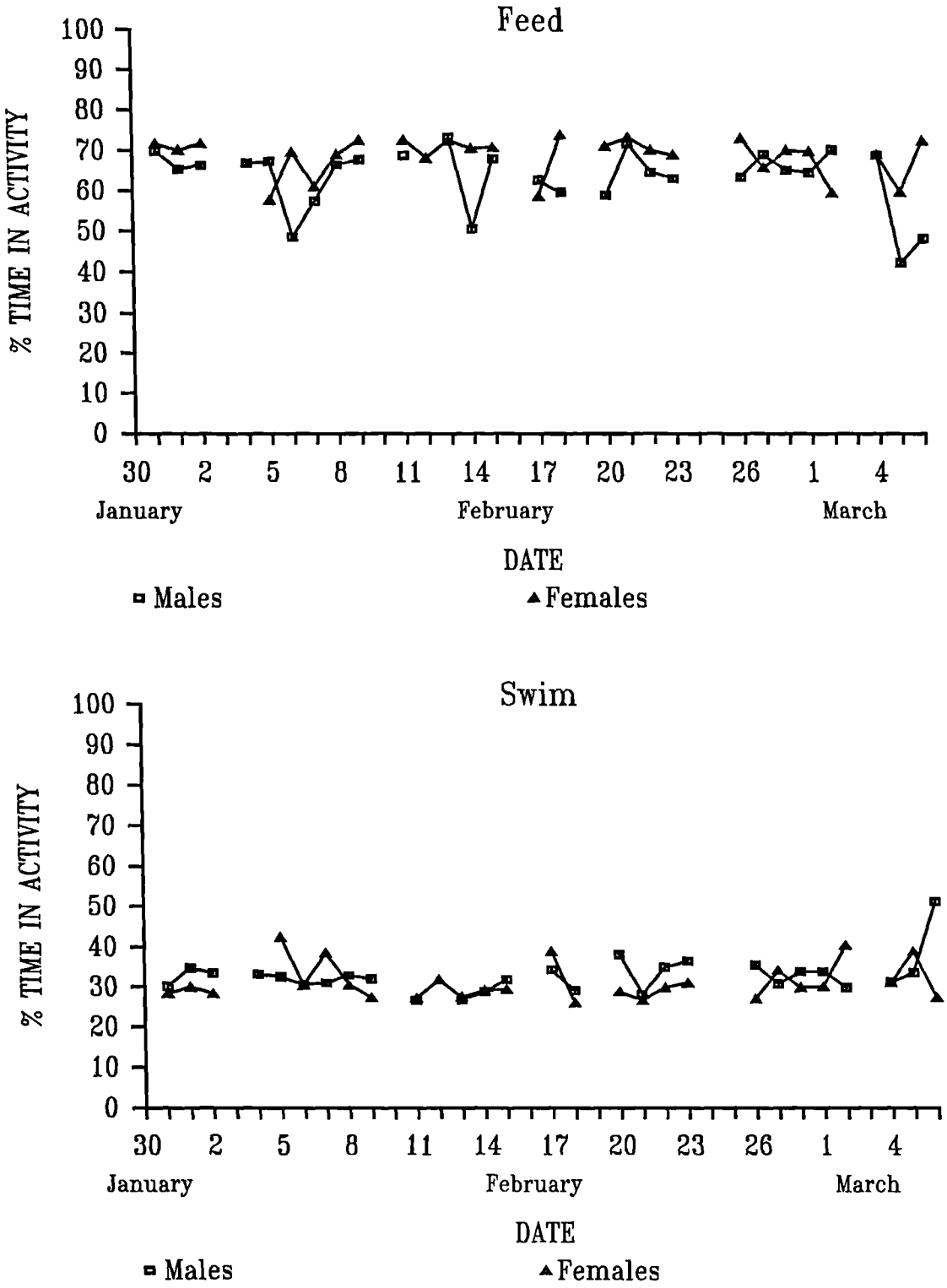

FIGURE 2.9. Change in nocturnal activity of Ruddy Duck wintering at CVL with date.

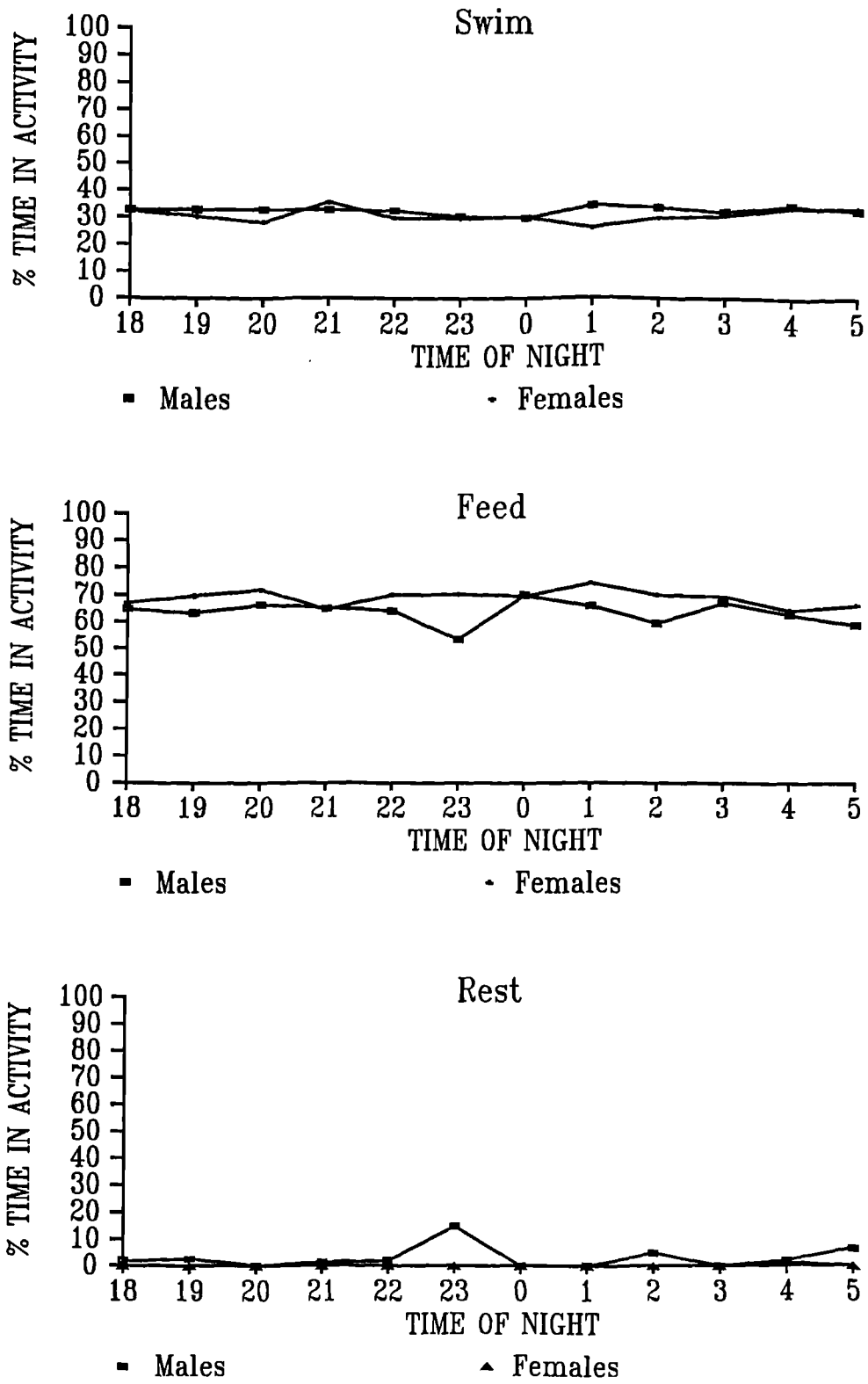

FIGURE 2.10. Change in nocturnal activity of Ruddy Duck wintering at CVL with time of night.

The Ruddy Ducks' nocturnal behaviour did not differ between morning and evening observation periods (MW U-Tests, $p>0.05$).

2.4.2.4 Effect of Weather on Behaviour

There were two periods of strong winds and rain during the study period, between 30 January and 8 February and between 26 February and 28 February. Wind speed exceeded force 4 on 16 days and there was rain on 14 days. Rain did not significantly affect the nocturnal behaviour of the Ruddy Ducks at CVL (MW U-Tests, $p>0.05$; Table 2.8). However, note that in males the decrease in the amount of time spent feeding in rainy conditions was accompanied by an increase in resting behaviour. In females/juveniles, this did not happen.

TABLE 2.8. Nocturnal time budget of Ruddy Duck wintering at CVL - direct effect of wind and rain on percent time spent in major behaviours. Means with different letters are significantly different (MW U-Tests, $p<0.05$).

	Actual Wind Speed				Rain			
	≤ Force 4		≥ Force 5		Present		Absent	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Males	N=113		N=35		N=26		N=122	
Swim	33.04 a	0.639	30.38 b	1.629	32.89	2.383	32.31	0.571
Feed	64.62	1.060	61.39	3.299	58.55	3.667	64.99	1.099
Rest	1.57	0.729	7.05	3.690	6.78	4.26	2.04	0.881
Females/ juveniles	N=64		N=24		N=13		N=75	
Swim	31.47	0.802	29.14	0.771	30.87	1.791	30.83	0.673
Feed	68.19	0.940	70.81	0.785	68.77	2.082	68.93	0.777
Rest	0.19	0.193	0	0	0	0	0.17	0.165

Males spent significantly less time swimming in windy conditions (MW U-Test, $p<0.05$), but the amount of time which females/juveniles spent performing the two major behaviours was unaffected (Table 2.8). Although the difference was not significant, males spent more time resting in windy conditions, whereas females/juveniles did not.

There was no significant difference in the behaviour of males and females/juveniles when the effect of wind speed was examined on a nightly basis, either when the data were analysed using the three different categories described in section 2.3.3 (KW Tests, $p>0.05$) or when categories 2 and 3 were combined and compared with category 1.

The ambient temperature during the study period varied between -1 and 13°C with a median value of 7°C. When the data were divided into the three temperature groups, below median temperature, at median temperature and above median temperature, there was no significant difference in the Ruddy Ducks' behaviour between the three groups (KW Tests, $p>0.05$). Ambient temperature and daily mean temperature were not significantly correlated with either of the major behaviours of males or females/juveniles (Table 2.7). A plot of nocturnal activity against temperature showed that the level of swim and feed behaviour remained constant as temperature changed (Figure 2.11).

The visibility of the moon did not have any effect on the birds' behaviour. Neither males nor females/juveniles showed significantly different levels of major behaviours under conditions of low ($\leq 4/8$) and high ($\geq 5/8$) cloud cover or between situations when the moon was visible or obscured/below the horizon (MW U-Tests, $p>0.05$).

There were no significant correlations between moon phase or days since last new moon and either of the major behaviours of males or females/juveniles, but females/juveniles did show a significant positive correlation between swim and days since last full moon and a significant negative correlation between feed and days since last full moon (Table 2.7). Males showed a similar trend in behaviour with days since last full moon, that is, a positive correlation for swim and a negative correlation for feed, but the correlations were not significant.

2.4.3 Diurnal Dive Time Analysis

The depth of water at diurnal feeding sites varied from 1.5 to 5.0m. Feeding occurred over a large area of the southern section of the lake with apparently no preferred sites. Birds were, however, observed to dive repeatedly at certain sites after previously moving some distance while diving.

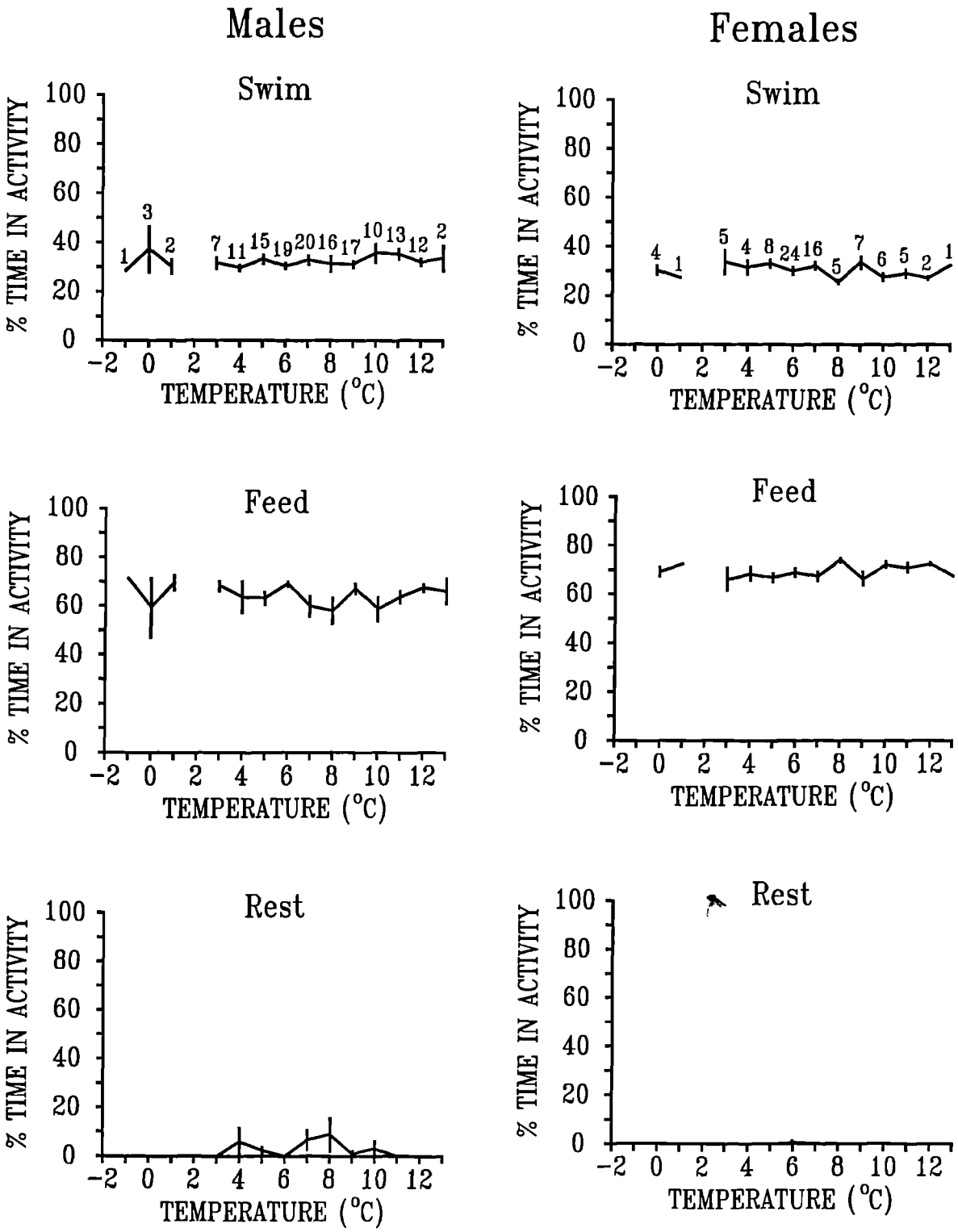

FIGURE 2.11. Change in nocturnal activity of Ruddy Duck wintering at CVL with temperature. Vertical bars represent ± 1 S.E.. Sample sizes are given above error bars.

Non-parametric statistics were used for analysis as the dive and inter-dive time data were non-normally distributed even after suitable transformations had been applied (Shapiro-Wilk Test for normality). For the same reason, regression analyses were not applied to diurnal dive/inter-dive analyses.

A total of 455 dives from 64 feeding bouts from a maximum of 35 birds (ten alternate males, ten basic males and 15 females) met the selection criteria and were selected for analysis. Mean dive and inter-dive lengths were 30.53 (± 0.774) seconds and 12.04 (± 0.361) seconds for alternate males, 27.17 (± 0.634) seconds and 10.95 (± 0.299) seconds for basic males and 26.64 (± 0.566) seconds and 11.13 (± 0.315) seconds for females/juveniles (Table 2.9).

TABLE 2.9. Diurnal dive length and associated inter-dive interval of Ruddy Duck wintering at CVL. Means with different letters are significantly different between age/sex classes (MW U-Test, $p<0.05$).

Age/sex Class	N	Dive Length				Inter-dive Length			
		Mean	S.E.	Max.	Min.	Mean	S.E.	Max.	Min.
Alternate Males	99	30.53 a	0.774	45.2	6.8	12.04 a	0.361	28.4	4.4
Basic Males	172	27.17 b	0.634	47.8	4.8	10.95 b	0.299	33.4	3.0
Females/ juveniles	184	26.64 b	0.566	47.2	2.4	11.13 b	0.315	32.8	1.0

Both dive length and inter-dive interval differed significantly between the age/sex classes (KW Tests: Dive, $p<0.001$; Inter-dive, $p<0.01$). Alternate males had significantly longer dives and inter-dive intervals than the other age/sex classes (MW U-Tests, $p<0.05$). The dive times of basic males and females/juveniles were not significantly different. In view of these results, the three age/sex categories were treated separately in further analyses.

All three age/sex categories of Ruddy Duck showed significant positive correlations between date and dive length (Table 2.10), but only females/juveniles showed a similar relationship with inter-dive length. When the same test was performed using mean daily

dive and inter-dive lengths, only alternate males showed a significant positive correlation with dive length (Spearman's correlation, r_s=0.893, N=7, p<0.01) and only females/juveniles with inter-dive (Spearman's correlation, r_s=0.643, N=12, p<0.05). Time of day was positively correlated with dive length for basic males and females/juveniles, but not for alternate males. Females/juveniles also showed a significant positive correlation between time of day and inter-dive interval. Alternate males and females/juveniles exhibited longer dives in warmer ambient temperatures, but the inverse was true for basic males. There was a negative correlation between dive length and feeding bout number for basic males whilst alternate males showed the opposite trend.

TABLE 2.10. Diurnal time budget of Ruddy Duck wintering at CVL - Spearman's correlation coefficients between dive and inter-dive length and feeding bout number, date, time of day and ambient temperature. *, p<0.05; **, p<0.01; ***, p<0.001.

	N	Feeding Bout No.	Date	Time of Day	Ambient Temperature
Alternate Males					
Dive	99	0.212 *	0.697 ***	-0.109	0.272 *
Inter-dive	99	-0.113	-0.093	0.083	-0.072
Basic Males					
Dive	172	-0.155 *	0.371 ***	0.418 ***	-0.177 *
Inter-dive	172	0.113	0.058	-0.033	-0.167 *
Females/juveniles					
Dive	184	0.032	0.278 ***	0.220 **	0.341 ***
Inter-dive	184	0.134	0.226 **	0.179 *	0.230 **

There was no significant dive/inter-dive time correlation for any of the age/sex classes. No dive/inter-dive plots were constructed due to a small sample size per data point.

There were no significant differences between the dive frequencies per feeding bout of the different age/sex classes or the associated dive intensities (KW Tests, p>0.05), although alternate males tended to have less dives per bout than the other classes (Table 2.11). Length of feeding bout and the number of feeding bouts per observation period (per bird) did not differ significantly between the age/sex classes (KW Tests, p>0.05).

TABLE 2.11. Diurnal time budget of Ruddy Duck wintering at CVL - dive frequency per feeding bout and associated dive intensity.

Age/sex Class	N	Dive Frequency Per Bout				Dive Intensity (Dives/min)			
		Mean	S.E.	Max.	Min.	Mean	S.E.	Max.	Min.
Alternate Males	18	5.50	0.506	10	3	1.48	0.095	2.95	1.15
Basic Males	22	7.82	0.986	19	4	1.54	0.047	1.97	1.20
Females/ juveniles	24	7.67	1.116	27	3	1.55	0.040	2.13	1.18

Mean dive length per feeding bout in both male categories increased significantly as the study period progressed, but females/juveniles showed no correlation (Table 2.12). There was also a positive correlation between mean inter-dive length per feeding bout and date in the female/juvenile category and a positive correlation between mean dive length per bout and time of day for basic males. No relationship was found between mean dive length and feeding bout number.

TABLE 2.12. Diurnal time budget of Ruddy Duck wintering at CVL - Spearman's correlation coefficients between mean dive and inter-dive length per feeding bout and feeding bout number, date, time of day and ambient temperature. *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$.

	N	Feeding Bout No.	Date	Time of Day	Ambient Temperature
Alternate Males					
Mean Dive	18	0.000	0.679 **	0.037	0.414
Mean Inter-dive	18	-0.121	-0.066	0.233	-0.027
Basic Males					
Mean Dive	22	-0.297	0.525 *	0.655 ***	-0.152
Mean Inter-dive	22	0.251	-0.072	-0.351	-0.147
Females/juveniles					
Mean Dive	24	-0.017	0.144	0.192	0.282
Mean Inter-dive	24	-0.053	0.513 *	0.058	0.161

The three age/sex categories did not differ significantly in the number of dives made per bird or the associated dive intensities (KW Tests $p>0.05$).

Date was positively correlated with mean dive length per study bird in alternate males and with mean inter-dive length per study bird in females/juveniles (Table 2.13). The only other significant correlation was a positive association between time of day and mean dive length per bird for basic males.

TABLE 2.13. Diurnal time budget of Ruddy Duck wintering at CVL - Spearman's correlation coefficients between mean dive and inter-dive length per study bird and date, time of day and ambient temperature. *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$.

	N	Date	Time of Day	Ambient Temperature
Alternate Males				
Mean Dive	10	0.880 ***	-0.139	0.336
Mean Inter-dive	10	-0.135	0.127	-0.098
Basic Males				
Mean Dive	10	0.499	0.721 *	-0.250
Mean Inter-dive	10	0.302	-0.285	-0.344
Females/juveniles				
Mean Dive	15	0.199	0.304	0.348
Mean Inter-dive	15	0.653 ***	0.200	0.315

The number of dives per feeding bout and the number of dives per bird were not correlated with date, time or ambient temperature for any of the age/sex classes (Table 2.14). However, there was a significant positive correlation between the number of feeding bouts per bird and date for alternate males and a negative correlation with time for basic males.

TABLE 2.14. Diurnal time budget of Ruddy Duck wintering at CVL - Spearman's correlation coefficients between dive frequency per feeding bout, dive frequency per bird, bout frequency per bird and date, time of day and ambient temperature. *, p<0.05; **, p<0.01; ***, p<0.001.

	N	Date	Time of Day	Ambient Temperature
Alternate Males				
Bout Dive Frequency	18	-0.120	0.282	0.115
Bird Dive Frequency	10	0.588	-0.134	-0.065
Bout Frequency	10	0.646 *	-0.363	-0.118
Basic Males				
Bout Dive Frequency	24	-0.298	0.018	0.352
Bird Dive Frequency	10	-0.310	-0.573	-0.252
Bout Frequency	10	-0.129	-0.744 *	-0.118
Females/juveniles				
Bout Dive Frequency	24	-0.300	-0.050	-0.096
Bird Dive Frequency	15	-0.465	0.191	-0.084
Bout Frequency	15	-0.129	0.378	0.177

2.4.4 Nocturnal Dive Time Analysis

The depth of water at the nocturnal feeding areas in Heron's Green Bay varied from 2.5 to 3.5m.

Non-parametric statistics were used for analysis as the dive and inter-dive time data were non-normally distributed even after suitable transformations had been applied (Shapiro-Wilk Test for normality). For the same reason, regression analyses were not applied to nocturnal dive/inter-dive analyses.

A total of 7460 dives from 462 feeding bouts from a maximum of 278 birds (169 males and 109 females/juveniles) met the selection criteria and were selected for analysis. Mean dive and inter-dive lengths were 27.76 (± 0.056) seconds and 10.91 (± 0.042) seconds for males and 26.52 (± 0.074) seconds and 10.18 (± 0.048) seconds for females/juveniles (Table 2.15). Males had significantly longer dives and inter-dive intervals than females/juveniles (MW U-Test: Dive, p<0.001; Inter-dive, p<0.001). In view of these results, males and females/juveniles were treated separately in further analyses.

TABLE 2.15. Nocturnal dive length and associated inter-dive interval of Ruddy Ducks wintering at CVL. Means with different letters are significantly different between age/sex classes (MW U-Test, $p<0.05$).

Age/sex Class	N	Dive Length				Inter-dive Length			
		Mean	S.E.	Max.	Min.	Mean	S.E.	Max.	Min.
Males	4395	27.76 a	0.056	58.40	9.93	10.91 a	0.042	26.80	3.82
Females/ juveniles	3065	26.52 b	0.074	44.00	7.94	10.18 b	0.048	27.60	3.20

Female/juvenile Ruddy Ducks showed a significant negative correlation between dive length and feeding bout number whilst both age/sex categories showed a significant negative correlation between bout number and inter-dive length (Table 2.16).

TABLE 2.16. Nocturnal time budget of Ruddy Duck wintering at CVL - Spearman's correlation coefficients between dive and inter-dive length and feeding bout number, date, time of day and ambient temperature. *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$.

	N	Feeding Bout No.	Date	Time of Night	Ambient Temperature
Males					
Dive	4395	-0.018	0.101 ***	-0.026	-0.027
Inter-dive	4395	-0.049 **	0.118 ***	-0.028	-0.081 ***
Females/juveniles					
Dive	3065	-0.053 **	0.078 ***	-0.091 ***	0.039 *
Inter-dive	3065	-0.040 *	0.164 ***	0.025	-0.085 ***

There were significant positive correlations between dive and inter-dive length and date for all age/sex classes, however, only males showed a significant positive correlation for inter-dive length when the analysis was repeated using mean daily dive values (Spearman's correlation, $r_s=0.695$, N=19, $p<0.01$). Time of night was significantly negatively correlated with dive length for females/juveniles, but there was no such relationship for males. Both age/sex categories showed a significant negative correlation between inter-dive time and ambient temperature whilst females/juveniles exhibited a

significant positive correlation between dive length and ambient temperature.

There was a significant positive dive time x inter-dive time correlation for both males and females/juveniles (Spearman's correlations, $p<0.001$), whether the data were expressed as original dive/inter-dive times (males: $r_s=0.087$, N=4395; females/juveniles: $r_s=0.174$, N=3065), mean dive/inter-dive times per feeding bout (males: $r_s=0.282$, N=300; females/juveniles: $r_s=0.447$, N=162) or mean dive/inter-dive times per bird (males: $r_s=0.373$, N=169; females/juveniles: $r_s=0.474$, N=109). However, because of individual variation, the proportion of the variation explained is very small. Figure 2.12 illustrates the significant positive correlation between dive length and inter-dive interval for males ($r_s= 0.406$, N=25, $p<0.05$) and females/juveniles ($r_s= 0.721$, N=21, $p<0.01$) when the data were grouped into one second dive length intervals. There is a gradual increase in inter-dive-interval with increasing dive length up to 32 seconds in males and 31 seconds in females. With further increase in dive length, the inter-dive interval levels off or even declines.

As stated above, the relationship between dive length and inter-dive pause is also apparent on an individual basis. Mean dive interval and mean inter-dive interval per bird are significantly positively correlated for males and females/juveniles (Fig. 2.13). Table 2.17 provides a comparison of the slopes of inter-dive against dive time plots for various waterbirds. The slope for female/juvenile Ruddy Ducks is less than that for males, however, no covariance analysis could be performed on the data as assumptions of the analysis could not be met. The slope is the among the lowest of all the diving ducks and considerably less than the values for the two members of the *Aythyini* tribe.

Females/juveniles had significantly higher dive frequencies and hence significantly higher dive intensities per feeding bout than males (MW U-Tests, $p<0.001$; Table 2.18). This was probably a simple effect of females having significantly longer feeding bouts (MW U-Test, $p<0.01$) and hence less feeding bouts per observation period (MW U-Test, $p<0.01$; Table 2.19).

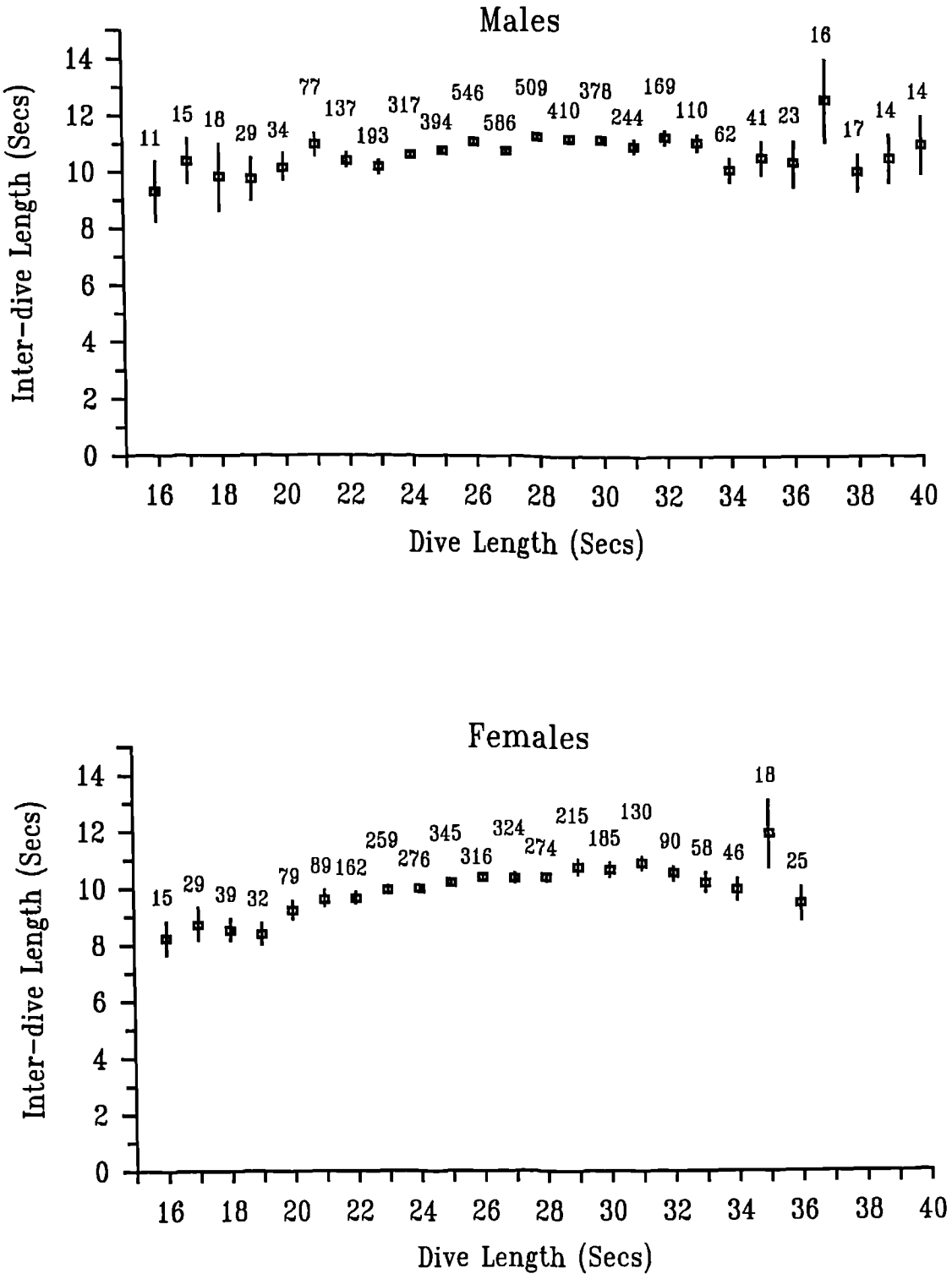

FIGURE 2.12. Relationship between nocturnal dive length and inter-dive length for male and female/juvenile Ruddy Duck wintering at CVL. Data points are mean inter-dive length per one second dive length (data points with n<10 excluded). Vertical bars represent ± 1 S.E.. Sample sizes are given above error bars.

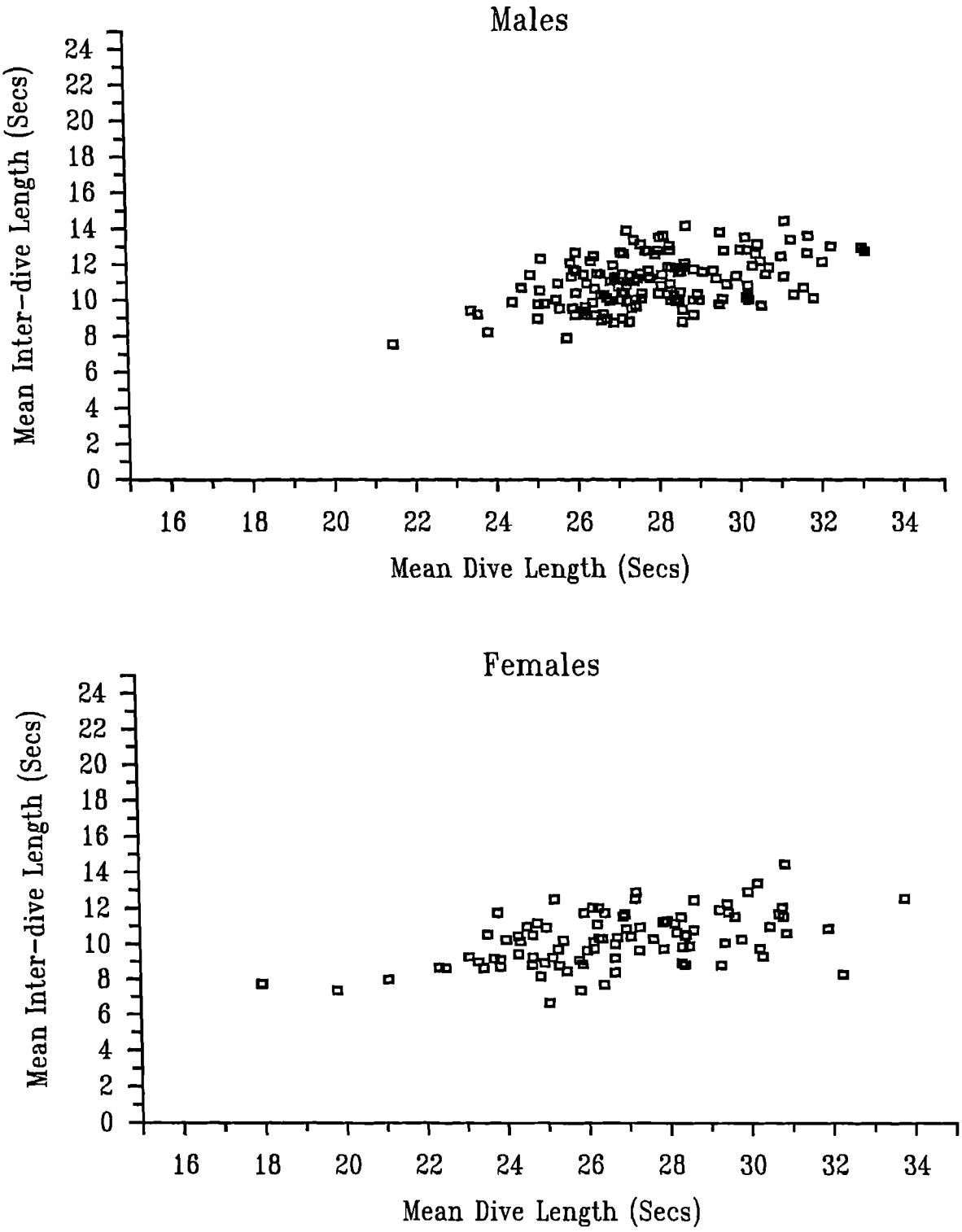

FIGURE 2.13. Relationship between nocturnal mean dive length and mean inter-dive length per bird for male and female/juvenile Ruddy Duck wintering at CVL.

TABLE 2.17. *Comparison of the inter-dive/dive time relationship in diving waterbirds.*

Species	Slope of Plot of Inter-dive against Dive	Reference
Diving Ducks - combined	0.64	Ydenberg (1986) using data from Dewar (1924)
Tufted Duck	0.55	Nilsson (1972)
Mergansers - combined	0.49	Ydenberg (1986) using data from Dewar (1924)
Ruddy Duck - Male	0.35	This study
Goldeneye	0.33	Nilsson (1972)
Rock Shag (full grown, Falklands, November 1989)	0.33	Wanless and Harris (1991)
Loons, Grebes, Cormorants and Alcids - combined	0.31	Ydenberg (1986) using data from Dewar (1924)
Ruddy Duck - Female/juvenile	0.29	This study
Long-tailed Duck	0.28	Nilsson (1972)
Rock Shag (full grown, Falklands, February 1990)	0.28	Wanless and Harris (1991)
Western Grebe	0.19	Ydenberg (1986), Ydenberg and Forbes (1988)

TABLE 2.18. Nocturnal time budget of Ruddy Duck wintering at CVL - dive frequency per feeding bout and associated dive intensity. Means with different letters are significantly different between age/sex classes (MW U-Test, $p<0.05$).

Age/sex Class	N	Dive Frequency Per Bout				Dive Intensity (Dives/min)			
		Mean	S.E.	Max.	Min.	Mean	S.E.	Max.	Min.
Males	300	14.65 a	0.661	51	1	1.55 a	0.008	2.12	1.08
Females/ juveniles	162	18.92 b	1.051	48	1	1.63 b	0.015	2.48	1.28

Mean dive length and inter-dive length per feeding bout increased significantly as the study period progressed in males and females/juveniles (Table 2.20). There was also a significant negative correlation between mean inter-dive length per feeding bout and ambient temperature in males. Time of night was not significantly correlated with either

TABLE 2.19. Nocturnal time budget of Ruddy Duck wintering at CVL - feeding bout length and feeding bout frequency (per observation period). Means with different letters are significantly different between age/sex classes (MW U-Test, $p<0.05$).

Age/sex Class	Bout Length (seconds)					Bout Frequency (Bouts/Obs. Period)				
	N	Mean	S.E.	Max.	Min.	N	Mean	S.E.	Max.	Min.
Males	300	566.5 a	25.43	1812.8	35.0	169	1.78 a	0.067	5	1
Females/ juveniles	162	694.2 b	37.63	1761.5	46.8	109	1.49 b	0.068	4	1

TABLE 2.20. Nocturnal time budget of Ruddy Duck wintering at CVL - Spearman's correlation coefficients between mean dive and inter-dive length per feeding bout and feeding bout number, date, time of day and ambient temperature. *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$.

	N	Feeding Bout No.	Date	Time of Night	Ambient Temperature
Males					
Mean Dive	300	0.059	0.151 **	-0.075	-0.043
Mean Inter-dive	300	-0.046	0.164 **	0.016	-0.133 *
Females/juveniles					
Mean Dive	162	-0.070	0.233 **	-0.080	0.020
Mean Inter-dive	162	0.005	0.319 ***	0.134	-0.080

mean dive or inter-dive length per feeding bout.

The two age/sex categories did not differ in the number of dives made per bird (MW U-Test, $p=0.193$). Mean dive length and inter-dive length per study bird were positively correlated with date in both sexes (Table 2.21). Again, there was a significant negative correlation between mean inter-dive interval per bird and ambient temperature for males, but no significant correlations with time of night for either sex.

The number of dives per feeding bout, the number of dives per bird and the number of feeding bouts per bird were not correlated with date, time of night or ambient temperature for either age/sex class.

TABLE 2.21. Nocturnal time budget of Ruddy Duck wintering at CVL - Spearman's correlation coefficients between mean dive and inter-dive length per study bird and date, time of day and ambient temperature. *, p<0.05; **, p<0.01; ***, p<0.001.

	N	Date	Time of Night	Ambient Temperature
Males				
Mean Dive	169	0.169 *	0.012	-0.059
Mean Inter-dive	169	0.204 **	0.053	-0.188 *
Females/juveniles				
Mean Dive	109	0.211 *	-0.103	0.034
Mean Inter-dive	109	0.268 **	0.078	-0.135

Both age/sex categories showed significantly longer dive times while feeding nocturnally compared with diurnal feeding activity (males: MW U-Test, $p<0.001$; females/juveniles: MW U-Test, $p<0.01$), whereas only females/juveniles showed significantly longer nocturnal inter-dive intervals (MW U-Test, $p<0.01$).

2.5 DISCUSSION

2.5.1 Methods

Statistical analysis of time budget data varies widely between studies. Many workers have used parametric statistics even though their data do not meet the assumptions of normality of distribution or homogeneity of variances. Others have performed arcsine transformations on proportional data and assumed that the resulting distributions are normal or "approximate to normal" without providing any statistical evidence. Non-parametric statistics are used throughout this study as all of the data analysed were non-normally distributed even after suitable transformations had been performed. This applies equally to, for example, arcsine-transformed time budget data or log-transformed dive times, even though the reasons for non-normality differed. Baldasarre *et al* (1988) reviewed time-activity budget methods, but did not consider the use of parametric versus non-parametric statistics. The use of non-parametric statistics is a time-consuming, but necessary, requirement of the analysis of time budget data if statistical assumptions are to be met. Consideration should also be given to the rejection from statistical analyses of behaviours which constitute only a small proportion of the total time budget.

Another important variation in the statistical treatment of time budget data arises from the length of the individual observation period or sampling unit. An individual observation period of 30 minutes was used in this study, whereas many other workers (eg. Alexander 1980; Bergan 1986) have used a five minute individual observation period. There are two important implications which result from this point.

1. The distribution of time budget data obtained using short individual observation periods will be more highly skewed which has implications for data transformation.

2. Perhaps the most important point is the increased sample size which results from using short individual observation periods, given that the individual observation period is used as the experimental unit. Spurious statistically significant results may occur simply as a result of large sample sizes. It would be useful if quoted sample sizes were accompanied by the total time of observation so misleading high sample sizes could be easily identified.

Many workers who have collected diel time budget data have combined diurnal and nocturnal data to produce a diel time budget. This is quite acceptable when the nocturnal and diurnal data are collected concurrently, however, the data in this study were not treated in this way for the following reasons:-

1. The two time budgets were collected in different winters and combining the data sets would have introduced variation due to the different environmental, biological and climatic conditions experienced during the two winters.

2. The diurnal and nocturnal data were collected at two different sites at CVL.

3. The limited range of the night-viewing equipment used during the nocturnal time budget resulted in the identification of fewer behaviours than in the diurnal time budget and, although differences will be small, the data will not be directly comparable for this reason.

4. Both time budgets amalgamated did not cover the full 24 hour cycle. There were

two two hour periods from which no observations were made: sunset (1600-1800h) and sunrise (0600-0800h). This was due to difficulty in observing distant birds in poor light conditions, disturbance of the Ruddy Ducks by roosting gulls and caution with the use of the night-viewing equipment which could have been damaged by use in high light intensity.

It is important to note that activities of the same name may not be directly comparable between studies. Behaviour categories of the same name differ considerably between this study and Alexander's (1980) study of the behavioural ecology and sociobiology of the *Aythyini*. Alexander did not recognise an alert category of behaviour and included alert activity in both resting and swimming categories depending on the locomotory state of the study bird. Alexander also construed drinking to be a comfort movement, whereas in this study it is included in the feeding category. Bergan (1986) followed Alexander's definitions and also did not recognise alert as a distinct class of activity. Swimming activity is another area where there is a great deal of variation in definition. The category in this study includes all types of swimming behaviour, such as loafing, locomotion and inter-dive interval. Other workers have defined "swim" in a number of different ways. For example, Alexander (1980) included birds in the sleeping posture in the "swim" category if they were changing their position in the resting flock, whereas this behaviour would have been recorded as "rest" in this study. Alexander also included loafing activity in his "resting" category, whereas in this study it would have been included in "swim". In some studies, the inter-dive interval has been included in feeding behaviour whilst in others it has been viewed as a mutually exclusive behaviour (Bergan 1986). It is important to realise the differences between posture-oriented definitions used in this study and state-oriented definitions used by workers such as Alexander.

2.5.2 Time Budgets

2.5.2.1 Sex-ratio

The sex-ratio of Ruddy Ducks wintering at CVL during the diurnal time budget was male biased. This disagrees with Cramp and Simmons (1977) who stated that the "sex-ratio at Avon lakes" is "more or less even". Male-biased sex-ratios have also been found in the American population of Ruddy Ducks during winter (Bellrose *et al* 1961), spring (Hochbaum 1944 (cited in H.Hays, unpubl. notes); Johnsgard and Buss 1956; H. Hays,

unpubl. data), summer (Gray 1980) and from data collected all year round (Low 1941; Glover 1951; Mumford 1954) or from an undefined time of year (Bellrose *et al* 1961). Only two studies have found a female-biased sex-ratio (Erickson 1943; Barcelona 1976). It is likely that the sex-ratio at CVL during the diurnal time budget was actually slightly higher than the observed level due to the inclusion of a small number of late moulting first year males in the female category.

2.5.2.2 Effect of Time of Day on Behaviour

Diurnal time budgets during the winter/non-breeding period have now been constructed for the majority of northern hemisphere anatids, but there is still very limited information on their nocturnal activity. Workers have recently realised the importance of the inclusion of nocturnal data in time budget analyses, especially as there may be fundamental differences between diurnal and nocturnal activity. One of the major differences between diurnal and nocturnal time budgets is the amount of time allocated to foraging behaviour. Many species have been found to forage more during the night (Teal - Tamisier 1974; Green-winged Teal *Anas crecca carolensis* - Tamisier 1976, Rave and Baldasarre 1989; Garganey - Tamisier 1976; Gadwall - Paulus 1984; Pintail *A. acuta* - Tamisier 1976; North American Black Duck *A. rubripes* - Morton *et al* 1989; Mottled Duck *A. fulvigula* - Paulus 1988a; Wigeon *A. penelope* - Campredon 1981; Shoveler - Pirot and Pont 1987; Pochard - Nilsson 1970b, Willi 1970; Scaup *Aythya marila* - Nilsson 1970b), others continue to forage at a similar rate to their diurnal activity (North American Black Duck - Jorde and Owen 1988) whilst there are also examples of ducks which either feed most during the day (Mallard - Jorde 1981 (cited in Jorde and Owen 1988); Ring-necked Duck *A. collaris* - Bergan *et al* 1989; Lesser Scaup *A. affinis* - Bergan *et al* 1989; Bufflehead *Bucephala albeola* - Bergan *et al* 1989; Eider *Somateria mollissima* - Nilsson 1970b; Long-tailed Duck *Clangula hyemalis* - Nilsson 1970b) or feed exclusively by day (Teal - Willi 1970; Red-breasted Merganser *Mergus serrator* - Sjöberg 1985; Goosander - Nilsson 1970b).

Other studies have found different feeding strategies for the same species under different environmental conditions or in different habitats. Eggeman and Jorde (unpubl. data cited in Jorde and Owen 1988) showed that Goldeneye *Bucephala clangula* wintering in coastal areas of Maine foraged nocturnally whilst three studies in other areas have shown them to feed mainly diurnally, namely birds wintering on Abberton Reservoir, Essex (Linsell

1969), on inland and coastal waters in southern Sweden (Nilsson 1970b) and on the Mississippi River (Sayler and Afton 1981). Nilsson (1970b) also found that Tufted Duck wintering in Sweden fed mainly during the night on the west coast and mainly diurnally in coastal areas in the south. Therefore the partitioning of feeding behaviour between the nocturnal and diurnal periods appears to be a flexible condition in ducks, rather than a fixed strategy. There is a wide range of variables affecting the choice of foraging period, all of which may be specific, not just to a certain species, but also to a certain site, habitat and time of year. These variables include food resources, lunar and tidal cycles, climatic conditions, physiological condition and body size constraints, activity of predators and extent of disturbance (Jorde and Owen 1988; Owen 1991).

The Ruddy Ducks at CVL were mainly inactive during the day, spending about 70% of their time asleep in roosting flocks. Similarly high levels of diurnal resting behaviour also occur in other Oxyurids. Non-breeding Maccoa Ducks *Oxyura maccoa* spent approximately 60% of the day resting (Siegfried *et al* 1976b) and White-headed Ducks *O. leucocephala* wintering in Spain rested for about 65% of the daylight hours (Amat 1984). The major diurnal behaviours of Ruddy Ducks at CVL were resting and swimming with lower levels of comfort movements and feeding. The fact that feeding constituted only 6.8% of the diurnal time budget (or about 9.6% if the inter-dive interval is included) strongly suggested that the Ruddy Ducks at CVL were feeding mainly during the night. This hypothesis was supported by the findings of the nocturnal time budget which showed that males and females/juveniles spent the vast majority of the hours of darkness in foraging activity. Assuming the amount of feeding behaviour shown by Ruddy Ducks in the two hour transitional period around dawn and dusk which were not covered by the winter time budgets was negligible, then males and females/juveniles performed approximately 92.7 and 94.2% of their feeding activity at night. This assumption is probably valid as Ruddy Ducks wintering at CVL spent these periods moving between preferred loafing and feeding sites. About one hour prior to sunset the roosting flocks of Ruddy Ducks began to break up and the birds moved to preferred nocturnal feeding sites. Sometimes this movement occurred earlier in the day, especially if gulls flying in to roost on the lake arrived early and harassed the ducks. This often happened on overcast days or days when there was bad weather. Bergan (1986) also noted a break up of rafts of resting Ruddy Ducks about 1 hour before sunset, but in the absence of disturbance by roosting gulls.

Only Shoveler (Pirot and Pont 1987), Teal (Tamisier 1974) and Tufted Duck (Pedroli 1982) have been shown to perform such a high proportion of their feeding behaviour at night (Owen 1991). It is important to note, however, that Ruddy Ducks in this study may have been feeding preferentially in the bay where the nocturnal time budget data were collected. This was suggested by the habits of the birds observed, notably their tendency to swim some distance to and from the bay to feed in the inner section close to the west shore. Whether or not this is actually the case, Ruddy Ducks undoubtedly spend a much higher proportion of their time feeding during the night compared with during the day.

There has only been one previous time budget study constructed for Ruddy Ducks during the winter. Bergan *et al* (1989) observed Ruddy Ducks at Par Pond Reservoir, a completely undisturbed site in South Carolina, during 1985 and 1986. They also found that Ruddy Ducks fed most at night (41% compared with 31% during the day), but the difference was not nearly as marked as at CVL. Stark (1978) found that Ruddy Ducks wintering in Pennsylvania fed mainly during the night and early morning, but he made no attempt to quantify this. Ruddy Ducks in captivity have also been found to be nocturnally active (Carbonell 1983).

Bergan *et al* (1989) also found that Ring-necked Duck, Lesser Scaup and Bufflehead all fed nocturnally, but at a lower level than during the day. The reason for this difference could be explained by the complete lack of disturbance at Par Pond allowing a higher level of diurnal feeding. Equally, the increased amount of diurnal feeding of Ruddy Ducks at Par Pond compared with CVL could be explained in the same way, however, diurnal disturbance at CVL is low during the winter, therefore this explanation probably does not apply. It is perhaps worth noting that Bergan *et al* (1989) based their nocturnal results on only 16 hours of data. Other workers have suggested that diurnal disturbance is important in regulating the amount of nocturnal feeding in diving ducks. Nilsson (1970b) suggested that the nocturnal feeding activity of Tufted Duck, Scaup and Pochard wintering in southern Sweden may be a response to disturbance on the diurnal feeding grounds. Unfortunately, his findings are based on feeding flight observations without any quantitative nocturnal data. Disturbance may also have been responsible for Tufted Duck wintering on Swiss lakes feeding almost exclusively during the night (Pedroli 1982). There is undoubtedly many other factors to consider, not least of all the availability and activity of prey species (see below).

The reasons for preferential nocturnal feeding in Ruddy Ducks are speculative. There is no reason to suggest that predation pressure plays any part because healthy Ruddy Ducks have no predators during the winter, not even humans as Ruddy Ducks are not yet valid quarry species in Great Britain. It is also unlikely that sensory factors are involved as Ruddy Ducks are mainly tactile feeders (Tome and Wrubleski 1988). Tamisier (1974) and Jorde and Owen (1988) suggested that it should be advantageous to waterfowl to conserve energy during the day and concentrate heat-generating activities to the cooler nocturnal period. It is possible that this theory could apply to Ruddy Ducks at CVL, but the most plausible explanation for preferential nocturnal feeding in Ruddy Ducks is the availability and activity of their main prey item, chironomid larvae (Siegfried 1973b; Bellrose 1976; Tome 1981; Gray 1980; Hoppe *et al* 1986; Woodin and Swanson 1989), although there is no hard evidence on which to base this statement and to prove such a hypothesis would be very difficult.

It is well known that many species of chironomids show a nocturnal pattern of adult emergence (Wool and Kugler 1969; Wrubleski and Ross 1989 and others). Many species of chironomids at Delta Marsh, Manitoba showed a significant negative correlation between extent of adult emergence and light intensity (Wrubleski and Ross 1989). In the same study, temperature was also significantly negatively correlated with adult emergence. An increase in waterfowl activity during periods of adult chironomid emergence has already been documented. At times of high adult emergence, dabbling ducks in Sweden and Wigeon in Norway both exhibited an increase in feeding activity (Sjöberg and Danell 1982; Jacobsen 1991), however, this is not of direct relevance to Ruddy Ducks which mainly feed on larvae present in the lake benthos.

Chironomid larvae in lake ecosystems have an increased level of planktonic activity during the hours of darkness (Mundie 1959; Hamilton 1965; Walker 1970) whilst stream-dwelling larvae show an increased rate of downstream drift during the night (Ali and Mulla 1979). The larvae have also been shown to vary their depth in the water column during daylight hours in response to light intensity (Luferov 1971). This light sensitivity varies with light intensity, temperature and larval maturity. Although he did not state the time of year in which his observations were made, Luferov (1971) found that first and second instar larvae of many chironomid species concentrated in better lighted areas during the day causing a daily vertical migration to the water surface during the day and

to the lake bottom at night. Third and fourth instar larvae were less light demanding and remained deeper in the water column or the lake benthos. Luferov (1971) also stated that larvae dwelling in the substrate remained there during periods of high light intensity (1100-1500h) then moved upwards as light intensity decreased (1500h onwards). If substrate-dwelling larvae are present at depths greater than 6-7cm during the day, they would effectively be unavailable to foraging Ruddy Ducks which have a maximum bill length of 44mm (Borrero and Hemández-Camacho 1958; Delacour 1959; Palmer 1976). As they migrate into the water column in late afternoon they would become available to foraging Ruddy Ducks.

In summary, the two situations which occur as night falls, the descent of larvae to the lake bottom and the ascent of substrate-dwelling larvae into the water column, could present an increased level of availability to foraging Ruddy Ducks. This may suggest that preferential nocturnal feeding behaviour in Ruddy Ducks is a response to the increased availability of chironomid larvae during the hours of darkness. Bergan (1986) proposed a similar explanation for preferential nocturnal feeding in Ruddy Ducks in South Carolina. He suggested that the nocturnal activity of the Phantom Midge *Chaeoborus punctipennis*, which migrates *en masse* from bottom sediments at sunset, could be linked to the Ruddy Ducks nocturnal feeding behaviour. Laughlin (1975) also suggested that the nocturnal feeding activity of Tufted Duck at Loch Leven could be due to increased availability of chironomid larvae. Furthermore, he also suggested that low numbers of Tufted Duck in winter occurred as a result of the cessation of the planktonic activity of the larvae.

It appears to be accepted now that, in favourable environmental and climatic conditions when food is not limiting, most diving ducks tend to exhibit some degree of nocturnal feeding, but whether this is a preferred strategy or an obligation caused by other factors may not be clear. Owen (1991) concluded his review of nocturnal feeding in waterfowl with the view that "foraging by night in the majority of waterfowl is perhaps most appropriately viewed as a less preferred strategy than feeding by day". It is difficult to apply such logic to the feeding behaviour of Ruddy Ducks wintering at CVL because their feeding habits appear to be governed by prey availability. As stated above, the partitioning of diurnal and nocturnal feeding varies between, and even within, species and the factors affecting the partitioning are many and complex.

2.5.2.3 Effect of Sex on Behaviour

There were no significant differences in behaviour for any of the age/sex categories of Ruddy Duck during the diurnal time budget, but females/juveniles spent significantly more time feeding and less time swimming than males during the night. Many time budget studies of non-breeding waterfowl have found no difference in behavioural investment between the sexes (Green-winged Teal - Quinlan and Baldasarre 1984, Rave and Baldasarre 1989; Gadwall - Paulus 1984, Gaston and Nasci 1989; Mallard - Turnbull and Baldasarre 1987; Mottled Duck - Paulus 1988a; American Wigeon *Anas americana* - Turnbull and Baldasarre 1987; Pochard -Klíma 1966; Lesser Scaup - Gammonley and Heitmeyer 1990; Bufflehead - Gammonley and Heitmeyer 1990). However, in some work females have been shown to spend more time feeding than males during the day (Pintail - Miller 1985; Canvasback *Aythya valisineria* - Hohman and Rave 1990, Lovvorn 1990; Ring-necked Duck - Bergan *et al* 1989; Lesser Scaup - Bergan *et al* 1989; Goldeneye - Nilsson 1970b) whilst in others the converse is true (Canvasback - Alexander 1980; Ring-necked Duck - Alexander 1980).

It is apparent from the above information that the difference in behavioural investment between the sexes varies depending on site, habitat, season and the many variables mentioned in section 2.5.2.2. Female Canvasback in freshwater habitats in Louisiana during the early and late winter periods fed more than males (Hohman and Rave 1990). Similarly, unpaired female Canvasback on spring migration at Lake Erie fed more than unpaired males (Lovvorn 1990). However, Alexander (1980) found that male Canvasback on coastal impoundments in South Carolina invested significantly more time in feeding behaviour than females. Female Ring-necked Duck fed more than males on Par Pond Reservoir, South Carolina (Bergan *et al* 1989), but the situation was reversed on coastal impoundments in the same state (Alexander 1980). Female Lesser Scaup fed more than males on freshwater habitats in South Carolina (Bergan *et al* 1989), but there was no difference found between the sexes in the same habitat in California (Gammonley and Heitmeyer 1990).

Although references concerned with sex differences in behaviour are quoted in this chapter from both diving and dabbling ducks, the two families are not directly comparable during the non-breeding season. This is because most diving ducks do not pair up until they reach their staging or breeding grounds, whereas pair formation in dabbling ducks occurs

on the wintering grounds. Pair formation may cause the sexes to differ in their behaviour if, for instance, the male spends more time in alert activity in relation to mate defence. Mate defence can also cause a difference in the amount of time spent feeding in diving ducks. Paired males tend to synchronize their diving activity with that of their mate, but dive for shorter periods to ensure their mates are never present on the water surface alone. No Ruddy Ducks at CVL were paired during the study periods, in fact, display was only observed on three occasions, hence behavioural differences between the sexes were not affected by pairing status.

There are a number of accepted explanations as to why non-breeding female diving ducks show a higher level of feeding activity than males:-

1. Body size in relation to:-

   i) metabolic demands. Smaller females feed more as they require a greater amount of energy to remain at an optimal thermodynamic equilibrium (Calder 1974).

   ii) diving constraints. It is possible that larger males can remain underwater for longer periods of time and thus collect more food per dive than females. This may suggest that males can meet their daily energy demands with less feeding activity than females. This explanation is supported by the fact that female Ruddy Ducks spent significantly more time feeding during the night than males which had significantly longer dive times and inter-dive intervals (see section 2.4.4). The lower amount of daily feeding necessary in males could also be explained by males being more efficient at feeding than females, as has been found in captive Pochard under experimental conditions (Carbone 1992).

2. The need to lay down lipid stores necessary for egg-formation and incubation. If the acquisition of endogenous lipid reserves necessary for breeding begins on the wintering grounds, as it appears to in Ring-necked Duck wintering in Florida (Hohman *et al* 1988), then females will need to attain relatively higher body masses than males before migration.

Alexander (1980) suggested that the fact that female Lesser Scaup fed more than males

during the day could be explained in terms of higher metabolic demands resulting from their smaller body size.

The second hypothesis given above may not be important when applied to Ruddy Ducks feeding at CVL during January and February. Ruddy Ducks leave CVL during February and March (Vinicombe and Chandler 1982) and arrive on the breeding grounds in the last weeks of March. Pair formation takes place in April and first clutches are laid at the beginning of May, however, the majority of clutches are not initiated until the end of May or later. Females would therefore have a six week period on the breeding grounds in which to attain sufficient endogenous lipid reserves for egg-formation and incubation. Female Ruddy Ducks in Manitoba rely primarily on exogenous energy for breeding and spend three to four weeks accumulating nutrient reserves prior to breeding (Tome 1981). Given that dietary intake on the breeding grounds provides the majority of nutrients for reproduction in female Ruddy Ducks in Manitoba, it seems unlikely that they should develop lipid reserves for breeding requirements while still on the wintering grounds in England. These considerations may, however, become important if Ruddy Ducks remain longer on wintering areas, as they appear to in South Carolina (Bergan *et al* 1989).

Selection pressures should favour birds which perform the most efficient migratory flights, that is, those birds with the minimum level of stored lipids necessary to reach the breeding grounds. This explanation may be somewhat confounded by the fact that the British population of Ruddy Ducks is descended from the North American population which usually migrates for much greater distances than the British birds. Obviously this situation depends on whether the controlling mechanism for the process of premigratory fattening in Ruddy Ducks is endogenous, modified by the migratory situation of the birds involved or a combination of the two.

Female Pochard wintering at Abberton Reservoir, Essex are initially in poor physical condition relative to males, probably because of insufficient time to replenish lipid reserves before migration from their Siberian breeding grounds. They then gain body mass at a faster rate (and presumably feed more) than males during the premigratory period yet only achieve a similar percentage gain in body mass by the time of their departure (Fox *et al* in prep). This would support the hypothesis that the premigratory reserves acquired by both sexes only provide energy for migratory flight.

Whatever the reason for the higher level of nocturnal feeding in female/juvenile Ruddy Ducks, it is apparent that they needed to feed constantly during the hours of darkness, whereas males can afford to spend a small proportion of their time resting.

2.5.2.4 Effect of Date on Behaviour

During the non-breeding period, waterfowl show a characteristic change in activity as the season progresses (Paulus 1988b). They typically feed most upon their arrival on the wintering grounds in order to restore reserves which have been used up during the previous breeding season and migration and to lay down new reserves for the ensuing winter. The mid-winter period is usually typified by a decrease in feeding activity and a corresponding increase in other less energy-demanding behaviours, such as resting. Feeding activity increases again in late winter due to premigratory hyperphagia, reduced food availability and in preparation for breeding. Perry *et al* (1986) argued that this pattern of behaviour was governed by an endogenous rhythm because captive Canvasback fed *ad libitum* diets still showed reductions in feed intake, activity and body mass during mid-winter. They also observed similar mid-winter loss in body mass, despite *ad lib.* diets, in Redhead *Aythya americana*, North American Black Duck and Mallard. Endogenous rhythms of change of body mass have also been suggested for North American Black Duck (Reinecke *et al* 1982) and Canada Goose *Branta canadensis* (Williams and Kendeigh 1982). However, Joyner *et al* (1984) provided experimental evidence that captive Canada Geese did not show any endogenous rhythm of body mass change. Geese fed on *ad lib.* diets gained mass steadily through the winter whilst those fed on restricted diets lost mass in the mid-winter period. This suggests that body mass in mid-winter varies in response to the available food supply. Similarly, Hohman *et al* (1988) found that Ring-necked Duck wintering in Florida showed a steady gain in mass as the season progressed. Milne (1976), Peterson and Ellarson (1979) and Kaminsky and Ryan (1981) have all suggested a similar explanation for mid-winter change in mass in waterfowl. Owen *et al* (in press) showed that Barnacle Geese *Branta leucopsis* in Dumfriesshire suffered a net energy deficit in mid-winter when quality and biomass of food was lowest. They also modelled body mass changes through the winter using intake rates and estimated energy expenditure and found that body mass predictions were consistent with observed mass and body condition changes although they did not provide any statistical evidence to support their hypothesis.

The winter study periods at CVL were too short to detect any seasonal changes in activity and although the Ruddy Ducks at CVL showed significant correlations between their major diurnal behaviours and date these were probably a consequence of a correlation between date and days from full moon (see below). Closer examination of the change in behaviour with date in both the diurnal and nocturnal time budgets suggested that the Ruddy Ducks were exhibiting a cyclical pattern of activity. This type of behaviour pattern has never previously been investigated, and hence observed, in any species of waterfowl. Most workers have simply lumped data into a number of season categories and investigated differences between those categories.

Plots of the major diurnal behaviours against date show what appears to be a cyclical pattern (Fig. 2.6). This is borne out by significant positive correlations between days from the change in behaviour (days since last full moon) and comfort movements, swim and feed and a significant negative correlation with rest. Plots of nocturnal behaviour against date are less convincing in this cyclical quality although females/juveniles showed a significant positive correlation between days since last full moon and swim and a significant negative correlation with feed. Males showed similar correlations but these were not significant. Nevertheless, it appears that as the number of days from the last full moon increases, nocturnal feeding in Ruddy Ducks decreases and diurnal feeding increases. It is possible that Ruddy Ducks show this apparently lunar cycling of their feeding behaviour in response to lunar cycling in the activity, and hence availability, of their main prey species, chironomid larvae. Feeding activity has been found to be correlated with prey activity in visually-feeding waterbirds. Great-crested Grebes on a freshwater lake in the Netherlands (Piersma 1988) and Goosanders and Red-breasted Mergansers on a Swedish river (Sjöberg 1985) showed peaks of foraging behaviour corresponding to peaks of activity in their major prey species. Assuming that chironomid larvae are more accessible to Ruddy Ducks at night and assuming that this is the main reason for the Ruddy Duck's nocturnal feeding habits, if chironomid larvae show a lunar cycle of activity, in which they are most available immediately following the full moon, then Ruddy Ducks could feed more during the preferred hours of darkness and less during the day in order to meet their daily energy requirements.

Lunar cycles of activity are known for terrestrial and aquatic insects (Saunders 1976) and many intertidal invertebrates. A lunar cycle of foraging activity with a peak at the full

moon has been found in a nocturnal bee, *Sphecodogastra texana* (Kerfoot 1967) and a similar cycle of pit-building activity has been demonstrated in the ant-lion, *Myrmeleon obscurus* (Youthed and Moran 1969). Hartland-Rowe (1955, 1958) demonstrated a lunar cycle of adult emergence in the mayfly *Povilla adusta* which showed a peak shortly after the full moon. This type of lunar cycle of emergence has also been demonstrated in lake-dwelling chironomids (Corbet 1958; Fryer 1959) which would support the theory of lunar cycling of behaviour suggested here. Corbet (1958) found that *Clinotanypus claripennis* and *Tanytarsus balteatus* showed lunar cycles of adult emergence with peaks just after the new moon whilst Fryer (1959) demonstrated that the African Midge, *Chironomus brevibucca*, exhibited a lunar cycle of emergence which peaked immediately following the full moon.

If Ruddy Ducks at CVL were feeding on chironomids which showed a similar lunar cycle of availability to that in *Chironomus brevibucca*, this could explain their apparent lunar cycle of behaviour.

The situation cannot be simply a response to light intensity as there was no relationship between moon phase, moon visibility or cloud cover and nocturnal feeding activity. The Ruddy Ducks' behaviour did not differ between periods when the moon was visible and absent or obscured or between conditions of low and high cloud cover and there was no significant correlation between moon phase and behaviour. However, it is possible that any effect of light intensity on the level of nocturnal feeding in the ducks was masked by the non-interactive nature of the non-parametric statistical analyses used.

It appears that true lunar cycles of behaviour have not been found in higher vertebrates, although Grasshopper Mice *Onchomys leucogaster breviauritus* (Jahoda 1973), a fruit bat, *Artibeus jamaicensis* (Morrison 1978) and the Galapagos Fur Seal *Arctocephalus galapagoensis* (Trillmich and Mohren 1981) reduce their activity during moonlit periods. Certainly, no lunar cycling of behaviour has been observed in waterfowl, although Barnacle Geese do show an increase in nocturnal feeding activity during the full moon (Ebbinge *et al* 1975; Ydenberg *et al* 1984) and a number of species show patterns of behaviour which are linked to tidal cycles (Paulus 1988b) and hence to the lunar cycle. Ydenberg *et al* (1984) also noted that the increase in nocturnal foraging in Barnacle Geese occurred independently of moon visibility.

It is possible that the high level of precipitation in the early part of the diurnal study period may have contributed to the increase in diurnal feeding behaviour, as feeding activity during the day was significantly higher in rainy conditions. However, as the increase in feeding behaviour in rainy conditions was not found in the nocturnal time budget, this explanation seems unlikely. In any case, this would not explain the cyclical quality of the plots of behaviour against date (Fig. 2.6).

2.5.2.5 Effect of Weather on Behaviour

2.5.2.5.1 General considerations

Most studies involving the construction of waterfowl time budgets have included considerations of how climatic variables influence behavioural investment. The effects of these variables are complex, difficult to measure accurately in terms of the actual microclimate experienced by the study bird and subject to manipulation from other influences, such as food availability, hence climatic variables only explain a small proportion of the observed variation in behaviour.

2.5.2.5.2 Wind

Ruddy Ducks showed significantly less diurnal feeding behaviour under conditions in which the wind speed exceeded force 4 on the Beaufort Scale. This difference was due to the birds' habit of seeking shelter in windy conditions in areas close to the shores of the lake where they did not feed to any great extent. The same trend was not apparent in the nocturnal time budget. Pintail (Miller 1985), Gadwall (Paulus 1984) and Mottled Duck (Paulus 1988a) have also been found to feed less in windy conditions, whereas North American Black Duck showed a significant positive correlation between feeding activity and wind speed (Morton *et al* 1989).

During the night, Ruddy Duck males at CVL spent significantly less time swimming in windy conditions, but the behaviour of females/juveniles was unaffected. Although not directly comparable with the "swim" category used in this study, locomotion and wind velocity were negatively correlated in Gadwall in Louisiana in winter (Gaston and Nasci 1989). The decrease in swimming activity shown by male Ruddy Ducks in windy conditions during the night was accompanied by an increase in resting, although this did not occur in females/juveniles which, despite the unfavourable climatic conditions, continued to feed. This adds weight to the hypothesis that female Ruddy Ducks cannot

meet their daily energy requirements without feeding continually during the night.

Bergan (1986) found no consistent effect of wind speed on the behaviour of Ruddy Ducks in South Carolina, although he suggested that the birds showed more feeding activity in rough water conditions caused by strong winds, which is contrary to the situation at CVL.

The indirect effect of wind speed on the nocturnal feeding behaviour of Ruddy Ducks was also investigated in this study. The hypothesis behind this analysis was that excessive wave action caused by severe gales, such as those experienced at CVL during the nocturnal time budget study, may cause a mixing of the bottom sediments and hence render potential prey items less available to the foraging Ruddy Ducks. If this was the case then feeding activity should have increased on days with excessive wave action, however, there was no significant difference in activity between the wind speed categories used in the analysis. It is likely that the Ruddy Ducks at CVL fed at depths at which the benthos was not agitated by wind action at the water surface and therefore the distribution of prey items was unchanged.

2.5.2.5.3 Rain

Precipitation was not monitored in detail during the diurnal time budget, but on days with prolonged showers, Ruddy Ducks spent significantly more time feeding. The nocturnal behaviour of Ruddy Ducks was found to be unaffected by rainfall. Studies on diving ducks, such as Bufflehead, Lesser Scaup and Ring-necked Duck (Bergan 1986), have found that feeding activity was positively correlated with rainfall, whereas the converse was true for dabbling ducks, such as Gadwall (Paulus 1984).

2.5.2.5.4 Temperature

Not surprisingly, temperature generally has the most effect of all weather variables on waterfowl behaviour during winter. At ambient temperatures below their LCT, all species are obliged to feed simply to maintain their thermoregulatory stability. At no time during either time budget study did the ambient temperature exceed the LCT of 13.1°C calculated for Ruddy Ducks. Therefore the birds in this study were at a constant thermoregulatory disadvantage. Given that this is the case, this lends more evidence, albeit circumstantial, to a thermoregulatory explanation of the significantly greater nocturnal feeding activity of smaller-bodied females/juveniles compared with males.

There were no significant differences between the amount of time spent feeding between the three temperature categories used in the analysis (below, at and above the median value) and there were no significant correlations between temperature and the major behaviours for any age/sex class in either of the time budgets. Ruddy Ducks did not show an increase in feeding activity as temperature declined. Bergan (1986) also found that temperature had no effect on the diurnal behaviour of Ruddy Ducks wintering in South Carolina.

This contrasts with studies of other species of waterfowl which generally report a negative relationship between feeding activity and temperature. Both Gadwall and Mottled Duck in Louisiana fed significantly more in temperatures lower than their LCT of 14°C and showed a negative correlation between feeding activity and temperature (Paulus 1984, 1988a). Significant negative correlations between feeding activity and temperature have also been found for North American Black Duck (Morton *et al* 1989), Gadwall (Gaston and Nasci 1989), Teal (Tamisier 1972), Bufflehead (Bergan 1986), Ring-necked Duck (Bergan 1986), Tufted Duck (Nilsson 1970b) and Goldeneye (Nilsson 1970b). Mallard also fed more in cold weather in winter in Nebraska (Jorde *et al* 1983; Jorde *et al* 1984) and Alabama (Turnbull and Baldasarre 1987).

2.5.3 Dive Times

Diurnal and nocturnal dive time analyses were performed separately for two reasons.

1. Birds were observed in two separate areas of the lake with different depths and surface areas. The diurnal observations were made over a large area of the southern section of the lake in a variety of depths usually exceeding 3.5m, whereas the nocturnal observations relate to a much smaller area of uniformly shallower water.

2. Birds appeared to differ in their foraging techniques between the sites. Diurnal dives were made over a larger area of the lake and birds surfaced further from their point of submergence than birds feeding at night which appeared to concentrate intensive diving activity in certain areas.

Alternate males had significantly longer diurnal dives and inter-dive intervals than basic males or females/juveniles and males had significantly longer nocturnal dive and inter-dive times than females/juveniles. Male-female differences in diving ability are well known in waterbirds, with males generally exhibiting longer dive times than females. This is the case for White-headed Duck wintering at Zóñar Lagoons, Spain (Amat and Sanchez 1982), breeding Long-tailed Duck in Greenland (Reynolds 1987), captive Pochard in England (Carbone 1992) and Pochard and Tufted Duck wintering on a reservoir in Germany (Willi 1970). However, no inter-sexual difference in dive lengths have been found for other species, such as Canvasback, Redhead, Ring-necked Duck and Lesser Scaup wintering on shallow coastal impoundments in South Carolina (Alexander and Hair 1979), Canvasback on spring migration in Wisconsin (Lovvorn 1990), Goldeneye wintering in coastal Scandinavia or inland Sweden (Nilsson 1969b) and Tufted Duck and Long-tailed Duck wintering on the coast of southern Sweden (Nilsson 1970a, 1972).

The greater diving ability of males is usually explained in terms of their larger body size giving them an energetic advantage over smaller bodied females, both in terms of physical ability and residual lung volume (O_2 storage capacity). A difference in dive times between birds in different plumages has not been previously noted, but this difference could also be explained in terms of the variation in diving ability of birds of different body size. It is possible that the basic male category may include smaller immature birds which have completed their pre-basic I moult and thus attained basic plumage, hence the smaller bodied, energetically disadvantaged argument would still apply. An equally plausible explanation relates to the condition of the birds in the two plumage categories. In captivity, healthy dominant male Ruddy Ducks acquire their alternate plumage earlier than less healthy or subordinate males (B. Hughes, unpubl. data). It is reasonable to assume that the situation is similar in the wild, therefore the first males to acquire alternate plumage are probably the "fittest" individuals with a consequently greater diving ability. This relationship between diving ability and stage of moult is also suspected for Pochard (C. Carbone, pers. comm.).

Nilsson (1970c) reported that in cold weather in winter in southern Sweden the male:female ratio of Goldeneye increased because males with a greater diving ability could continue to feed profitably in deep water areas when the shallows were frozen, whereas females could not and subsequently left the area. It is possible that the observed

differences in dive times between the sexes could be due, in part, to females preferentially feeding in shallower areas, as has been found for Ruddy Ducks, Bufflehead, Lesser Scaup and Ring-necked Duck in winter in South Carolina (Bergan and Smith 1989) and Goldeneye wintering in southern Sweden (Nilsson 1970b).

During periods of diurnal feeding, there was no difference between the age/sex categories in dive frequency and intensity per feeding bout or per bird, that is, alternate males, basic males and females/juveniles all performed roughly the same number of dives per feeding bout and per observation period. Total feeding bout length also did not differ significantly. Males and females/juveniles differed significantly in their nocturnal foraging. In summary, female/juvenile Ruddy Ducks showed a higher overall level of feeding behaviour (see section 2.4.2.1) and a higher frequency of significantly shorter dives in significantly longer feeding bouts than males.

Reynolds (1987) found that female Long-tailed Duck fed at a higher dive frequency than males and suggested this was "to compensate for shorter dive times", whereas Lovvorn (1990) found no difference in foraging rates of male and female Canvasback on spring migration in Wisconsin. Alexander (1980) also found that there was generally no difference in foraging rate between male and female Canvasback, Redhead, Ring-necked Duck and Lesser Scaup feeding on four shallow coastal impoundments in South Carolina. Female Redhead foraged at a faster rate than males at only one site. Alexander's results may be expected as the same study revealed no intersexual difference in dive times for any of the species. Curiously, the same author presented data from the same study in an earlier paper which showed that male Canvasback fed more frequently than females with no intersexual differences in Redhead (Alexander and Hair 1979). The addition of extra data not only changed Alexander's conclusions, but also considerably increased his observed foraging rates.

Perhaps not surprisingly, the dive times of male Ruddy Ducks at CVL were longer than those recorded at a shallower depth of 1-3m at Blithfield Reservoir, Staffordshire in January and April 1986, however, values for females/juveniles were similar (R.T. Joy, unpubl. data). Dive and inter-dive times at Blithfield were 21.91 (± 0.285) seconds and 11.31 (± 0.257) seconds for males (N=203, 21 birds) and 26.17 (± 1.894) seconds and 11.00 (± 0.685) seconds for females (N=12, 2 birds). Inter-dive times at CVL and

Blithfield Reservoir were similar. The longer dive times of females compared with males at Blithfield may well be an artefact of the small sample size. Heintzelman and Newberry (1964) quote a shorter mean dive time of (19.78 ± 0.23) seconds for a single unsexed Ruddy Duck feeding in an unspecified depth in New Jersey.

All age/sex classes of Ruddy Duck showed a significant positive correlation between both nocturnal and diurnal dive length and date whilst the same trend was apparent in both males and females/juveniles for nocturnal inter-dive interval. Similar trends were also present when the data were analysed as means per feeding bout and means per bird, however, if the data were analysed as daily mean dive and inter-dive lengths only alternate males during the day and males during the night showed significant positive correlations between date and dive length.

It appears that Ruddy Ducks wintering at CVL dive for longer periods of time when feeding later in the season. Captive Ruddy Ducks have longer dive times when feeding in more profitable patches of prey than in less profitable areas or areas devoid of food (Tome 1989). If the Ruddy Ducks' prey at CVL became more available as the study period progressed then this could explain the increase in dive length with date. Alternatively, the increase in dive time could be a means of increasing food intake to counteract the decrease in diurnal feeding activity as the winter progresses. Carbone (1992) also found that the dive times of Tufted Duck feeding on a gravel pit in Oxfordshire increased between January and May.

Correlations between dive/inter-dive length and time of day/night were inconsistent between age/sex classes, but the significant values suggested an increase in dive and inter-dive length with time during the day and a decrease as night progressed. However, because these trends are dissimilar between age/sex categories it is more likely that dive and inter-dive are not affected by time in a predictable manner.

Similarly changes in ambient temperature did not appear to affect the Ruddy Ducks' dive/inter-dive lengths in any predictable way. This is perhaps not surprising, considering that temperature had no effect on time spent in activity (see sections 2.4.1.4 and 2.4.2.4).

Ydenberg and Clark (1989) stated that anaerobic dives are regularly observed in nature,

but the only conclusive evidence they provided to support this statement referred to marine mammals. They proposed that an oxygen debt may be accumulated during a series of dives to be repaid later. Based on experimental evidence of oxygen consumption in captive Tufted Duck diving in an experimental tank, Butler and Stephenson (1987) proposed that there is no reason to believe that diving ducks are not able to perform all naturally occurring dives aerobically. In an earlier paper, Ydenberg (1986) suggested that the dive/inter-dive relationship of a diving bird depended on the mobility/availability of chosen prey species, that is, divers with mobile prey may postpone recovery until a series of dives has been completed, whereas birds feeding on sedentary prey seem to complete much more of the recovery after each dive. Whatever the theory behind the mechanics of diving in waterbirds, many studies have found a positive relationship between dive length and inter-dive interval (Stonehouse 1967; Nilsson 1969b, 1970a, 1970b; Morrison *et al* 1978; Ydenberg 1986; Ydenberg and Forbes 1988; Wanless and Harris 1991) whilst others have reported no relationship (Fjeldså 1973; Butler and Woakes 1979). Furthermore, it is generally accepted that unusually long periods underwater require proportionally longer periods at the surface for recovery (Butler and Stephenson 1987; cf. Nilsson 1970a, 1972; cf. Ydenberg 1986).

For three species of diving duck, Nilsson (1969b, 1970a, 1972) observed a steady increase in inter-dive interval with increase in dive time up to a point where birds needed relatively longer periods on the surface to recover. He proposed that this point indicated the longest normal dive time. This situation was apparent for Tufted Duck and Long-tailed Duck feeding in coastal areas of southern Sweden (Nilsson 1970a, 1972) and Goldeneye in a freshwater locality in the same country (Nilsson 1969b), but not for Goldeneye feeding on the coast (Nilsson 1970a, 1972). Nilsson attributed this lack of "exhaustion effect" in the latter case to the fact that these birds were not observed feeding at the limits of their diving capabilities. A similar explanation may be applicable to Rock Shags feeding in the Falkland Islands which showed a continuous linear relationship between dive time and inter-dive interval (Wanless and Harris 1991). This is perhaps not surprising, considering these birds were not observed for complete feeding bouts.

The data presented in this study show that an "exhaustion effect", as described by Nilsson (1969b, 1970a, 1972), is not apparent for Ruddy Ducks feeding nocturnally at CVL. The significant decrease in dive length for females/juveniles and inter-dive length for both

age/sex classes in successive feeding bouts may be a manifestation of increasing fatigue, but temporary satiation (Butler and Stephenson 1987) or decreasing profitability in successive feeding bouts (cf. Tome 1989) are equally plausible explanations.

Nilsson (1970a, 1972) suggested that the slope of the line from the plot of inter-dive versus dive time reflected the "efficiency" of diving ability. The lower the slope, the more "efficient" the diver or the shorter the inter-dive interval for a given dive time. On the other hand, Ydenberg (1986) proposed that the variation in slopes for different groups of diving birds reflected dietary preferences and different schedules of recovery from diving. Undoubtedly all three are important, but there are many other factors which can affect the variance in dive time/inter-dive time relationship. These include prey availability (Tome 1988), the presence of exploratory or unsuccessful dives in a feeding bout, extent of satiation and fatigue, influence of climatic variables, depth of water and interbout and interbird variation in diving ability.

Ruddy Ducks feeding nocturnally at CVL showed a similar slope of inter-dive interval against dive time as Nilsson's most "efficient" divers, Long-tailed Duck and Goldeneye (Table 2.17). This is considerably lower than values obtained for Tufted Duck (Nilsson 1970a, 1972), mergansers or a lumped category of diving ducks (Ydenberg 1986), but more than those for Western Grebes *Aechmophorus occidentalis* (Ydenberg 1986; Ydenberg and Forbes 1988). This would be expected (given that the slope of the plot of inter-dive interval against dive time does provide a crude measure of diving "efficiency") as Ruddy Ducks are most adapted to an aquatic lifestyle of all non-piscivorous diving ducks (Raikow 1973). The relatively high value calculated by Ydenberg for mergansers is perhaps surprising as they are also highly adapted to underwater foraging. Rock Shags showed a similar slope to Ruddy Ducks (Wanless and Harris 1991). Note that the inverse of the gradient of the line plot of inter-dive versus dive time will be comparable to the dive-pause ratio, which is often quoted by authors as a measure of diving ability (eg. Nilsson 1970a, 1972).

2.6 CONCLUSIONS - Time Budgets

Future time budget studies should take into account three fundamental considerations.

1. The need to collect an adequate amount of data. The fieldwork for most previous studies has been performed by individuals or pairs, whereas if more scientists were involved in a single study then continuous diel data could easily be collected. This would remove much of the speculation resulting from inadequate time sampling during activity budget studies (but may introduce observer error). Recent reviews of time-activity studies of wintering waterfowl have identified the need for the inclusion of adequate nocturnal sampling in time budget studies (Baldasarre *et al* 1988; Jorde and Owen 1988; Paulus 1988b). The problems associated with nocturnal observation are clear and well understood and workers should strive to overcome them. This should become less of a problem as night-viewing equipment and artificial light sources become more effective. Nocturnal and diurnal data should be collected together and if possible sufficient data for subsequent analyses should be collected in one season.

2. The testing of predetermined hypotheses. There have been many time budget studies performed on wintering Anatidae (see section 2.5.2), the vast majority of which have simply been descriptive or comparative whilst very few have set out to test predetermined hypotheses. As Paulus (1988b) points out, future studies must place emphasis on the testing of hypotheses. Simultaneous sampling of invertebrate populations must be one of the foremost aims of any future studies on the feeding ecology of wintering diving ducks.

3. The question of acceptable statistical analysis. There was little mention of statistical procedures in the recent reviews mentioned in the former paragraph. Baldasarre *et al* (1988) simply stated that "there was disagreement among investigators regarding statistical procedures for analysis of time-activity data" and "time-activity data should be subjected to a rigorous statistical analysis". Is it acceptable to simply insert a time budget data matrix into a large multivariate analysis or use parametric statistics for analysis even though the data do not meet the assumptions of these analyses? On the other hand, is it acceptable to spend the extra time necessary to analyse data using a series of non-parametric tests, which are non-interactive by definition and therefore cannot consider interactions between important factors in a complex ecological and biological situation? Workers should also consider the implications of the length of individual

observation periods. Using longer individual observation periods will reduce the noise in behavioural data and reduce the sample size thus presenting less chance of obtaining spurious significant results in subsequent data analysis.

All three recommendations strive to reduce the amount of controllable variation which is often inherent in time budget analysis whilst also illustrating the need for sound initial planning.

CHAPTER THREE.

DIURNAL TIME BUDGET OF MALE RUDDY DUCKS DURING THE COURTSHIP PERIOD AT MERE SANDS WOOD NATURE RESERVE, LANCASHIRE.

3.1 INTRODUCTION

The courtship behaviour of most male waterfowl is now well documented (e.g. Johnsgard 1965; Palmer 1976; Cramp and Simmons 1977; Madge and Burn 1988), although few studies have described the diurnal time budgets of male waterfowl during the courtship period. In most dabbling ducks, pair formation occurs on the wintering grounds and courtship takes place mainly in late autumn or early winter. Diving ducks usually delay pair formation until spring migration or after arrival on the breeding grounds, resulting in intensive courtship display in early spring.

In Great Britain, Ruddy Ducks have a relatively late and extended breeding season compared with other anatids. Birds usually arrive on the breeding grounds in mid-March and groups of males display to females until pair formation occurs in early April. The majority of young appear in June and July (Cramp and Simmons 1977).

Previous studies on Ruddy Ducks during the breeding season have concentrated on the energetic costs of breeding in females (Gray 1980; Tome 1981) and, although Gray (1980) performed an exhaustive analysis of the social behaviour of male Ruddy Ducks, she included little information on activity budgets. Only Ladhams (1977) has described the behaviour of courting male Ruddy Ducks in Great Britain.

This study aimed to determine the major behaviours of male Ruddy Ducks during the courtship period at Mere Sands Wood Nature Reserve (MSWNR) and examine the change in those behaviours with pairing status, time of day, date and temperature. Because of the high level of intraspecific interaction which occurs in Ruddy Ducks during the breeding season, the effect of the presence of other male and female Ruddy Ducks on male behaviour was also assessed.

3.2 STUDY AREA

MSWNR lies approximately 1km west of Rufford (53° 38'N, 2° 50'W) in the lowlands of West Lancashire (Fig. 3.1). Between 1974 and 1982 the central area of the original wood was cleared and the land subjected to commercial sand extraction leaving a peripheral band of mature woodland. Subsequent restoration of the quarried areas has provided an extensive system of lakes and areas of reed marsh covering about 42 hectares. After the sand extraction operations ceased in 1982, the ownership of the wood was transferred to the Lancashire Trust for Nature Conservation which now manages the reserve.

The reserve stands on stratified sand and peat overlying boulder clay. The upper soil layers are ground-water gley soils containing little organic matter and are characteristically associated with poor drainage. The surrounding woodland is comprised mainly of Birch *Betula pendula*, Oak *Quercus robur* and a large stand of Scots Pine *Pinus sylvestris*. Alder *Alnus glutinosa* is common in the wetter areas of the reserve with some Sallow *Salix caprea*, White Poplar *Populus alba* and Aspen *P. tremula*. The shrub layer is mainly Rhododendron *Rhododendron ponticum*. Lakeside vegetation is dominated by Soft Rush *Juncus effusus* with smaller areas of Hard Rush *J. inflexus*, Cattail *Typha latifolia* and Common Reed.

There are nine distinct areas of open water in the reserve (Fig. 3.2), some of which are interconnecting. All except the northern end of the Mere End, which is not shielded from the reserve footpath, are free from human disturbance and there are six observation hides on the lakes. A Tower Hide on the Heath Lake was completed in 1990 and was not present during the study. The lakes have an average depth of about 2.5m and a maximum depth of 7m. The main area of shallow water on the reserve is the Wader Scrape which adjoins the Washing Well lake. Roach *Rutilis rutilis* and Rudd *Scardinius erythrophthalamus* are the main species of fish in the lakes and common breeding birds on the lakes include Great-crested Grebe, Little Grebe, Mallard, Coot *Fulica atra* and Moorhen *Gallinula chloropus*.

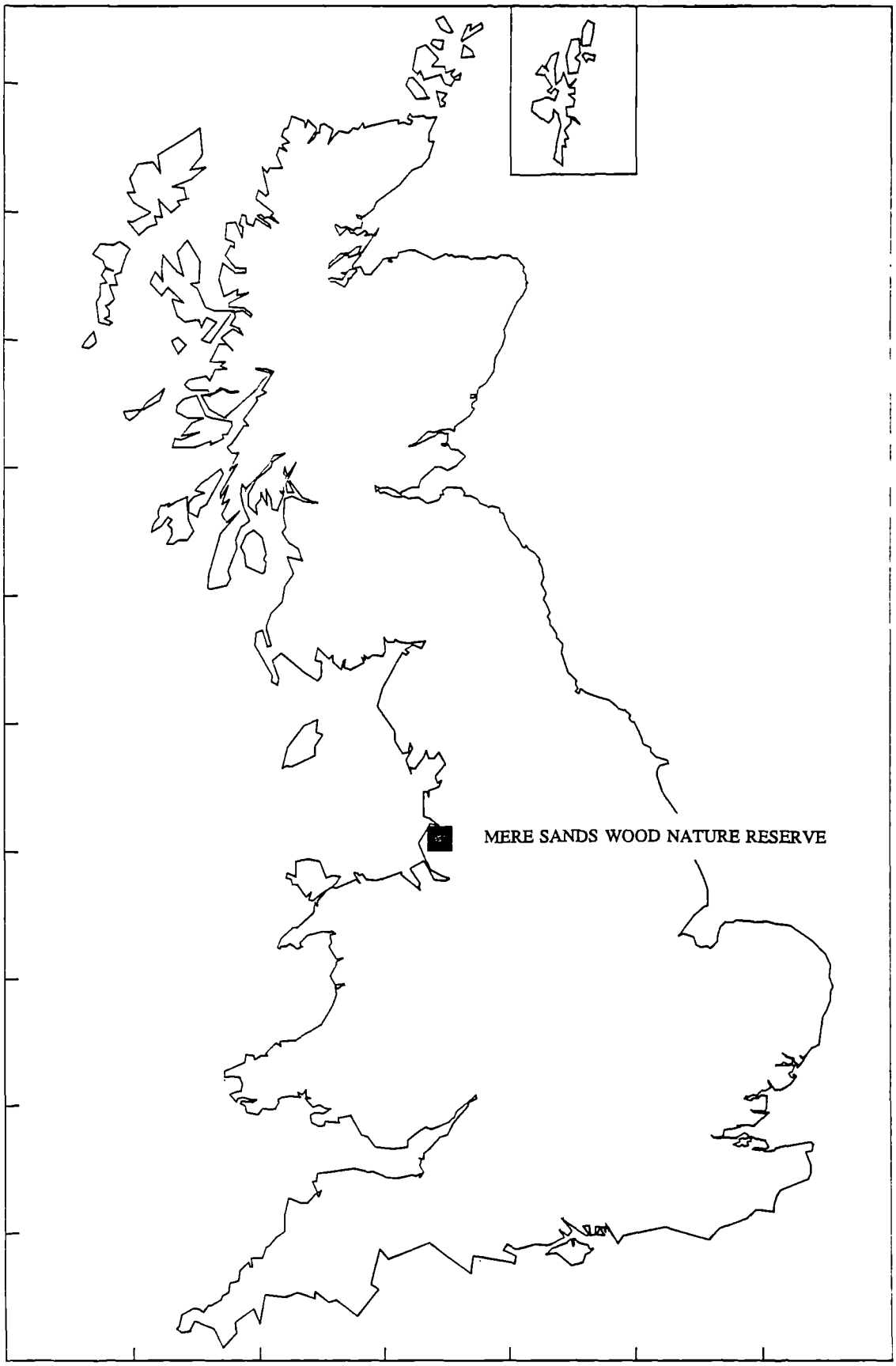

FIGURE 3.1. Location of MSWNR.

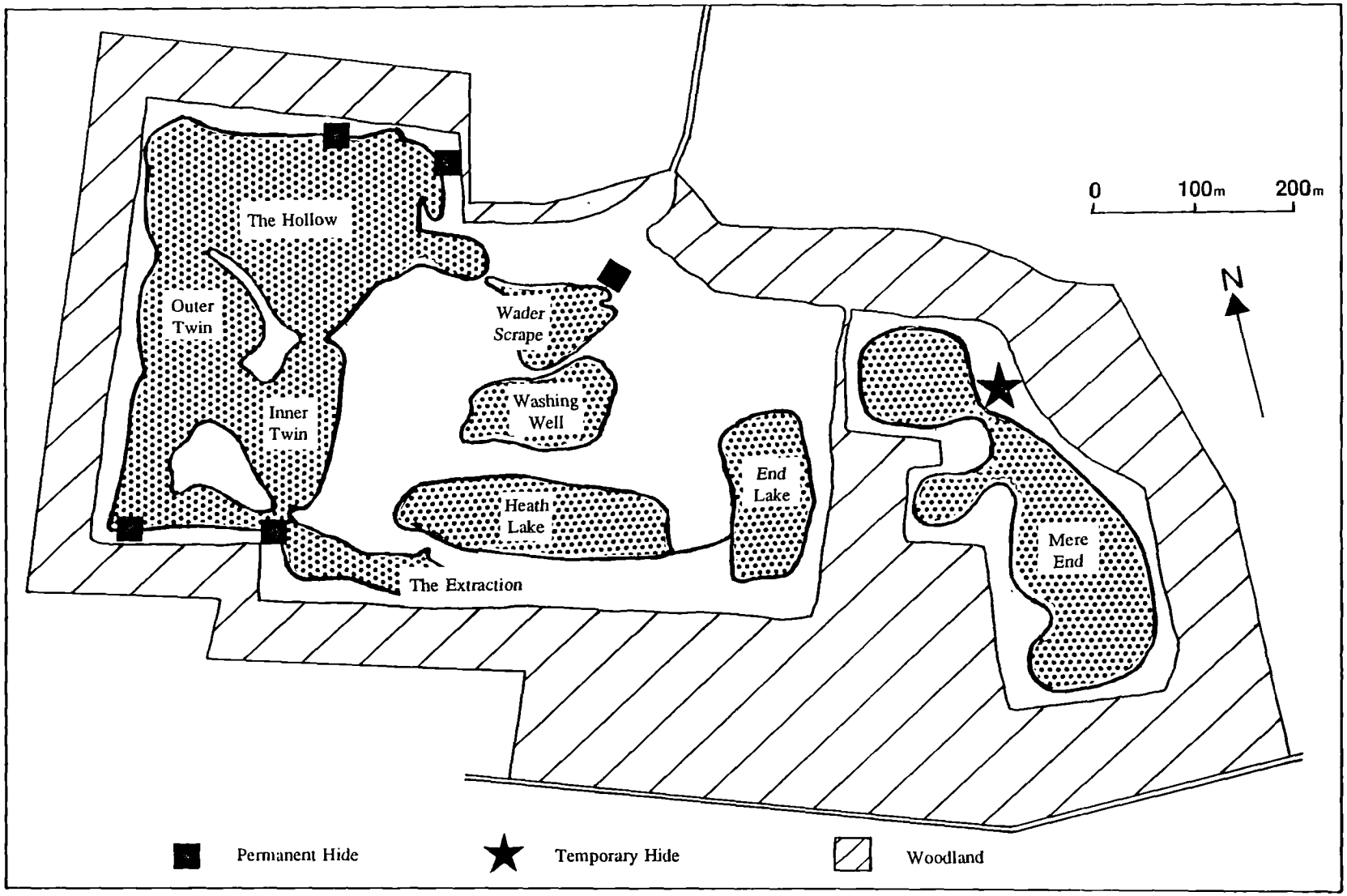

FIGURE 3.2. Map of MSWNR showing sites of observation during the male courtship display time budget.

3.3 METHODS

3.3.1 Diurnal Time Budget

Diurnal time budget data were collected between 17 March and 19 April 1989. To avoid the use of terms such as the spring arrival, pre-nesting or pre-laying phases, which have previously been defined in different ways, this period is referred to as the courtship period. All daylight hours, from 0600h until 1800h, were sampled once in a unit of two days. Methods of observation were identical to those used in the winter time budget studies (see Chapter Two).

Males on the Washing Well and Outer Twin were observed from permanent hides while a portable canvas hide was used to make observations on the Mere End (Fig. 3.2). Pairing status and the presence/absence of other male and female Ruddy Ducks were noted for each male under observation. Paired males were defined as males which continually associated with a female and defended her against the attentions of other males. Additional indications of paired status included inciting behaviour by the female and the synchronisation of diving behaviour of paired birds. As in Gray (1980), paired status does not imply a bonded association.

Ambient temperature was recorded for each male and maximum daily and overnight minimum ambient temperature were recorded on a daily basis.

The behaviours recorded were similar to those observed in Chapter Two with the following additions:-

COMFORT MOVEMENTS - **Rest-preen** - Also included:-
- **Wing-shiver.**

FEED - Also included:-

Head-under - Feeding in shallow areas of water with only the head submerged.

LAND - Presence on land while not performing any other behaviour. This was mainly loafing behaviour.

ALERT - Also included:-

Head Bob - While in head-up posture the head is bobbed once with the bill angled downwards in a similar manner to the initial stages of the bubbling display.

COURTSHIP DISPLAY - Descriptions of the sexual behaviour of male Ruddy Ducks are provided by many authors, including Johnsgard (1965), Joyner (1969), Gray (1980) and all standard texts on waterfowl. The following behaviours were included in the courtship display category:-

Bubbling Display - The major courtship display of the Ruddy Duck. The male assumes a head-up-tail-up posture with the ear-tufts raised and tracheal air sac fully inflated before beating the bill on the breast 6-12 times in an increasing tempo. Each beat is accompanied by a muffled popping noise and bubbles form around the breast from air forced from among the breast feathers. The neck is then stretched forwards as the tail is lowered, the folded wings raised slightly for a moment and the bill angled upwards and opened as a two-syllable "quack" is uttered.

Display Flight ("Ringing Rush" of Johnsgard 1965) - The male assumes a head-up-tail-up posture with the ear-tufts raised. He then flattens the ear-tufts and suddenly snaps down the partially spread tail into the water, extends the neck and skeeters over the surface of the water for 3-4m with the back hunched, flapping the wings. A popping sound is produced by the feet slapping the water (Miller *et al* 1977).

Surfboarding (Hunch Rush of Palmer (1976) and Hays unpubl. notes) - This courtship activity is exhibited by males when returning to a female, often after chasing away other males. The male swims towards the female with the rear of the body submerged, the tracheal sac inflated, the scapulars raised, the neck drawn back and the bill on the breast. In this posture, the male "surfboards" back to the female, producing a conspicuous wake of water.

Courtship Alert - Head-up-tail-up posture with ear-tufts erect. This behaviour mainly consisted of the Tail Flash display noted by other authors (Johnsgard 1965; Palmer 1976; Hays unpubl. notes). It was not possible to quantify Tail Flash as

a separate behaviour in this study because of the variation in the orientation of this display. While assuming the Tail Flash posture the male usually swims in front of the female with the tail raised and white undertail coverts exposed. The male appears to be attempting lead the female and strives to remain directly in front of her by manoeuvering his whole body to keep the white undertail coverts directed towards her. At MSWNR, males in the Tail Flash posture often swam alongside females or in other positions relative to the females without the undertail coverts directed towards them, therefore I recorded all of these postures as Courtship Alert behaviour.

Courtship Comfort Movements - All of these behaviours are performed with the ear-tufts erect and are ritualised versions of comfort movements.

> **Bill-dip-head-flick** (Bill Flicking of Johnsgard 1965) - This is a ritualised version of the comfort movement bill-dip, in which males dip the bill into the water, withdraw it and shake the head from side to side. However, this display is slower and more deliberate than the comfort movement and there is a forward jumping movement as males dip the bill in the water.
>
> **Rolling-cheeks-on-back** - A ritualised version of the comfort movement rolling-cheeks-on-back.
>
> **Tail Shake** - This behaviour is performed while in the Courtship Alert posture.
>
> **Wing Buzz** - A previously undescribed behaviour, in which the male assumes the Courtship Alert position then quickly "buzzes" the wings in a ritualised version of the comfort movement wing-shiver. In this behaviour, the wings are raised to the same position as that at the end of the bubbling display and not simply shuffled while in the rest position as in wing-shivering.

Courtship Dive - During sequences of display behaviours, males often performed shallow dives in which they were submerged for less than one second.

Courtship Swim - Displaying males sometimes swam close to their mates with the ear-tufts erect.

Copulate

A total of 46 behaviours were observed and amalgamated into ten mutually exclusive categories for analysis (Table 3.1). Four of the behaviours were performed on both land and water, but for the purpose of the analysis land and water categories were combined.

For brevity, males observed on the Washing Well may be referred to as WW males, males on the Outer Twin as OT males and males on the Mere End as ME males.

3.3.2 Data Analysis

As in Chapter Two, the number of records of each behaviour were expressed as a percentage of the total records for each observation period. Any mutually exclusive behaviour category which constituted ≥2.5% of the total diurnal time budget was defined as a major activity and selected for further analysis.

Four temperature variables were included in the analysis: actual ambient temperature, mean daily ambient temperature, maximum daily ambient temperature and overnight minimum ambient temperature. In a further investigation of the effect of temperature on the birds' behaviour, the data were separated into observations below, at and above median temperature.

To examine the effect of date on the males' behaviour, the study period was separated into two intervals: early courtship period from 17 March to 1 April and late courtship period from 2 April to 19 April 1989.

The data were analysed using the SYSTAT computer package (Wilkinson 1987). Data when birds were out of sight and observation periods less than 10 minutes long were excluded from the analysis. Sample sizes in the statistical procedures refer to the number of observation periods and all other statistical methods were similar to those used in Chapter Two.

TABLE 3.1. Behaviours exhibited by male Ruddy Duck at MSWNR during the courtship period. L denotes behaviour performed on land.

REST	- Sleep	
	- Pseudosleep	
COMFORT MOVEMENTS	- Preen (L)	
	- Roll-cheeks-on-back	
	- Rest-preen	
	- Foot-shake	
	- Tail-shake	
	- Wing-shiver	
	- Scratch	
	- Stretch	
	- Bill-dip (L)	
	- Bathe	
	- Wing-shiver (L)	
	- Minor comfort activities	- Yawn
		- Foot-shake
		- Tail-shake
		- Head-shake
SWIM	- Loaf	
	- Locomotion	
	- Inter-dive interval	
ALERT	- Head-up	
	- Extreme head-up	
	- Extreme head-up-tail-up	
	- Head bob	
FEED	- Dive	
	- Dabble	
	- Drink (L)	
	- Head-under	
LAND (L)		
COURTSHIP DISPLAY	- Bubble	
	- Display flight	
	- Surfboarding	
	- Courtship alert	
	- Courtship preen	- Bill-dip-head-flick
		- Roll-cheeks-on-back
		- Tail-shake
		- Wing buzz
	- Courtship dive	
	- Courtship swim	
	- Copulate	
SOCIAL INTERACTION	- Intraspecific	- initiated by study bird
		- initiated by another bird
	- Interspecific	- initiated by study bird
		- initiated by other species
	- Unknown species	
FLY		
SKEETER		

3.4 RESULTS

3.4.1 Diurnal Time Budget

The study period consisted of 30 study days and a total of 180 hours of observation provided 107.86 hours of usable data on a maximum of 15 male Ruddy Ducks. Approximately 15 hours of data were lost due to problems with the event recorder.

Non-parametric statistics were used in the analysis as examination of probability plots for the major behaviours showed the data to be non-normally distributed even after angular transformations had been performed.

Feeding (51.25 ± 1.474%), swimming (26.26 ± 0.637%) and resting (14.85 ± 1.783%) constituted most of the males' diurnal time budget during the courtship period (Table 3.2).

TABLE 3.2. Diurnal time budget of male Ruddy Duck on three lakes at MSWNR during the courtship period. Means with different letters are significantly different between sites (MW U-Tests, $P<0.05$).

	Washing Well		Outer Twin		Mere End		All Sites	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Major Behaviours								
Rest	16.32 a	3.136	7.29 b	2.524	20.24 a	3.330	14.85	1.783
Comfort Movements	3.54 a	0.561	1.81 b	0.314	3.44	0.048	2.96	0.274
Swim	28.21 a	1.167	26.88 b	0.946	23.81 c	1.119	26.26	0.637
Feed	46.41 a	2.570	57.94 b	2.248	49.89	2.650	51.25	1.474
Courtship Display	3.90	1.018	5.50 a	1.190	2.22 b	0.574	3.82	0.550
Minor Behaviours								
Alert	0.41	0.117	0.21	0.068	0.18	0.049	0.27	0.048
Social Interaction	0.29	0.071	0.30	0.065	0.10	0.046	0.23	0.036
Fly	0.01	0.01	0	-	0	-	Tr	-
Skeeter	Tr	-	0.01	0.014	0	-	0.01	0.01
Land	0.91	0.521	0.06	0.040	0.12	0.105	0.37	0.181
Total Time Watched (Hrs)	34.91		33.88		39.07		107.86	
No. of Observation Periods	89		83		92		264	

Courtship display (3.82 ± 0.550%) and comfort movements (2.96 ± 0.274%) were the other major behaviours. Minor behaviour categories were alert, social interaction, fly, skeeter and land.

Males on the three lake areas differed significantly in all of their major behaviours (MW U-Tests, $p<0.05$) and were therefore treated separately in further analyses. OT males fed significantly more and performed comfort movements significantly less often than WW males whilst they rested significantly less than birds on the two other sites. WW males swam significantly more than OT males which, in turn, swam significantly more than ME males. OT males displayed significantly more than ME males.

Subdivision of the data set, because of the significant differences in male behaviour between sites, meant that no further subdivisions in the data set could be made without reducing the sample sizes to an unacceptable level.

3.4.2 Effect of Paired Status on Behaviour

The first paired males were observed on 2 April 1989. There was no significant difference in behaviour between paired and single male Ruddy Ducks on the Washing Well or the Outer Twin (Table 3.3) with paired and single birds on the Washing Well having noticeably similar time budgets. Paired ME males rested significantly more and fed significantly less than single ME males. Paired OT males also rested more than single OT males but the difference was not significant. On all three sites, paired males displayed less than single males but not to any significant extent. A comparison of the time budgets of paired and single males after the day the first paired bird was observed showed no significant differences in behaviour. In general, paired males tended to rest more and feed and display less than single males.

3.4.3 Effect of the Presence of Other Male and Female Ruddy Duck on Behaviour

There were approximately 15 male and ten female Ruddy Ducks present at MSWNR during the study, which resulted in the majority of observations involving males present. WW males rested significantly less and swam significantly more in the presence of other male Ruddy Ducks (Table 3.4), but this result should be viewed with caution because of

TABLE 3.3. Diurnal time budget of paired and single male Ruddy Duck on three lakes at MSWNR during the courtship period. For each site, means with different letters are significantly different between pairing statuses (MW U-Tests, $P<0.05$).

	Washing Well				Outer Twin				Mere End			
	Paired		Single		Paired		Single		Paired		Single	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Rest	15.44	3.087	16.67	3.757	10.77	4.952	5.61	2.887	28.15 a	5.788	14.92 b	3.863
Comfort Movements	2.64	0.780	3.90	0.729	1.48	0.354	1.97	0.434	4.40	0.977	2.80	0.445
Swim	29.94	2.121	27.54	1.396	24.91	1.446	27.83	1.205	24.39	2.143	23.41	1.210
Feed	47.31	4.780	46.06	3.070	59.79	3.863	57.05	2.779	41.68 a	4.334	55.41 b	3.159
Courtship Display	3.32	1.658	4.12	1.266	2.68	1.250	6.86	1.634	0.81	0.369	3.17	0.909
Total Time Watched (Hrs)	9.83		25.08		11.57		22.31		16.89		22.18	
No. of Observation Periods	25		64		27		56		37		55	

TABLE 3.4. Diurnal time budget of male Ruddy Duck on three lakes at MSWNR during the courtship period with and without the presence of other males. For each site, means with different letters are significantly different (MW U-Tests, $P<0.05$) between male presence/absence categories.

	Washing Well				Outer Twin				Mere End			
	Males Present		Males Absent		Males Present		Males Absent		Males Present		Males Absent	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Rest	13.01 a	2.834	62.09 b	17.146	7.56	2.615	0	-	23.05	4.285	15.87	5.281
Comfort Movements	3.59	0.594	2.92	1.427	1.80	0.322	1.99	1.699	3.58	0.664	3.22	0.665
Swim	29.46 a	1.083	10.89 b	5.002	26.89	0.981	26.67	1.316	24.33	1.521	23.00	1.624
Feed	48.03	2.550	23.99	11.916	57.44	2.313	71.34	1.904	46.67	3.404	54.89	4.145
Courtship Display	4.18	1.086	0	-	5.71	1.229	0	-	1.77	0.553	2.93	1.192
Total Time Watched (Hrs)	31.92		2.99		32.71		1.17		24.19		14.88	
No. of Observation Periods	83		6		80		3		56		36	

the small sample size for the males absent category. Males on the other two lake areas behaved similarly with and without the presence of other males, but again there was a small sample size for the males absent category in OT males.

On the Outer Twin, females were present in all observations so it was not possible to investigate the effect of female presence on male behaviour at this site. WW males showed no significant difference in behaviour with and without female Ruddy Ducks present whilst ME males rested significantly more and fed significantly less in the presence of females (Table 3.5). There was more courtship display in both WW and ME males in the absence of females, but the differences were not significant.

TABLE 3.5. Diurnal time budget of male Ruddy Duck on two lakes at MSWNR during the courtship period with and without the presence of females. For each site, means with different letters are significantly different between female presence/absence categories (MW U-Tests, $P<0.05$).

	Washing Well				**Mere End**			
	Females Present		**Females Absent**		**Females Present**		**Females Absent**	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Rest	13.92	3.552	21.04	6.142	24.81 a	4.097	7.29 b	4.443
Comfort Movements	3.25	0.692	4.13	0.964	3.56	0.593	3.10	0.752
Swim	29.21	1.305	26.24	2.313	23.72	1.427	24.04	1.476
Feed	48.65	2.918	42.02	4.997	45.71 a	3.145	61.74 b	4.079
Courtship Display	3.81	1.275	4.07	1.714	1.68	0.488	3.77	1.701
Total Time Watched (Hrs)	23.25		11.67		29.70		9.36	
No. of Observation Periods	59		30		68		24	

3.4.4 Effect of Time of Day on Behaviour

WW males displayed significantly more in the afternoon than in the morning, but all other comparisons between morning and afternoon behaviour were not significant (Table 3.6). Time of day was significantly negatively correlated with resting and significant positively correlated with courtship behaviours in WW males (Table 3.7). Time of day and

TABLE 3.6. Diurnal time budget of male Ruddy Duck on three lakes at MSWNR during the courtship period before and after noon. For each site, means with different letters are significantly different (MW U-Tests, $P<0.05$) between morning and afternoon categories.

	Washing Well				Outer Twin				Mere End			
	Morning		Afternoon		Morning		Afternoon		Morning		Afternoon	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Rest	21.84	5.192	10.92	3.435	8.22	4.091	6.38	3.035	18.14	4.633	22.08	5.100
Comfort Movements	2.78	0.545	4.29	0.967	2.45	0.577	1.18	0.231	3.12	0.528	3.72	0.825
Swim	25.76	1.832	30.61	1.383	28.22	1.611	25.58	0.990	24.75	1.497	22.98	1.701
Feed	46.60	3.745	46.23	3.568	55.35	3.516	60.47	2.807	51.14	3.911	48.79	3.879
Courtship Display	2.57 a	1.388	5.20 b	1.478	5.04	1.635	5.95	1.745	2.47	0.961	2.00	0.727
Total Time Watched (Hrs)	44		45		41		42		43		49	
No. of Observation Periods	17.98		16.94		17.53		16.34		17.70		21.37	

TABLE 3.7. Diurnal time budget of male Ruddy Duck on three lakes at MSWNR during the courtship period - Spearman's correlation coefficients between major behaviours and date, time of day and ambient temperature variables. *, P<0.05; **, P<0.01; ***, P<0.001.

	N	Time of Day	Date	Actual Ambient Temperature	Mean Daily Ambient Temperature	Max. Daily Ambient Temperature	Overnight Min. Ambient Temperature
Rest							
Washing Well	89	-0.252 *	-0.298 **	-0.328 **	-0.285 **	-0.295 **	-0.171
Outer Twin	83	0.007	0.085	0.216	0.243 *	0.174	0.324 **
Mere End	92	-0.031	0.275 **	-0.069	0.069	0.189	-0.071
Comfort Movements							
Washing Well	89	0.165	-0.113	-0.028	0.013	-0.004	-0.083
Outer Twin	83	-0.196	0.121	0.046	0.085	0.122	0.075
Mere End	92	-0.010	0.189	0.049	0.054	0.091	-0.033
Swim							
Washing Well	89	0.296 *	0.274 *	0.240 *	0.248 *	0.249 *	0.027
Outer Twin	83	-0.239 *	-0.013	-0.028	-0.005	0.069	-0.054
Mere End	92	-0.013	-0.061	-0.054	-0.144	-0.147	-0.115
Feed							
Washing Well	89	-0.010	0.184	0.230 *	0.141	0.171	0.269 *
Outer Twin	83	0.097	0.007	-0.157	-0.181	-0.202	-0.265 *
Mere End	92	0.024	-0.276 **	0.118	-0.039	-0.163	0.154
Courtship Display							
Washing Well	89	0.373 ***	0.149	0.198	0.198	0.189	-0.036
Outer Twin	83	0.069	-0.023	0.014	0.021	0.101	0.055
Mere End	92	-0.071	-0.120	-0.155	-0.126	-0.208 *	0.077

swimming were significantly negatively correlated in OT males and significant positively correlated in WW males. ME males showed no significant correlation between time of day and behaviour.

A plot of mean hourly behaviour against time of day (Figures 3.3a-c) illustrates the above correlations. Resting and feeding activity at all three sites fluctuated in an unpredictable manner during the day whilst swimming and comfort movements showed less severe fluctuations. At all three sites, courtship display showed peaks in early morning, late morning/early afternoon and late afternoon.

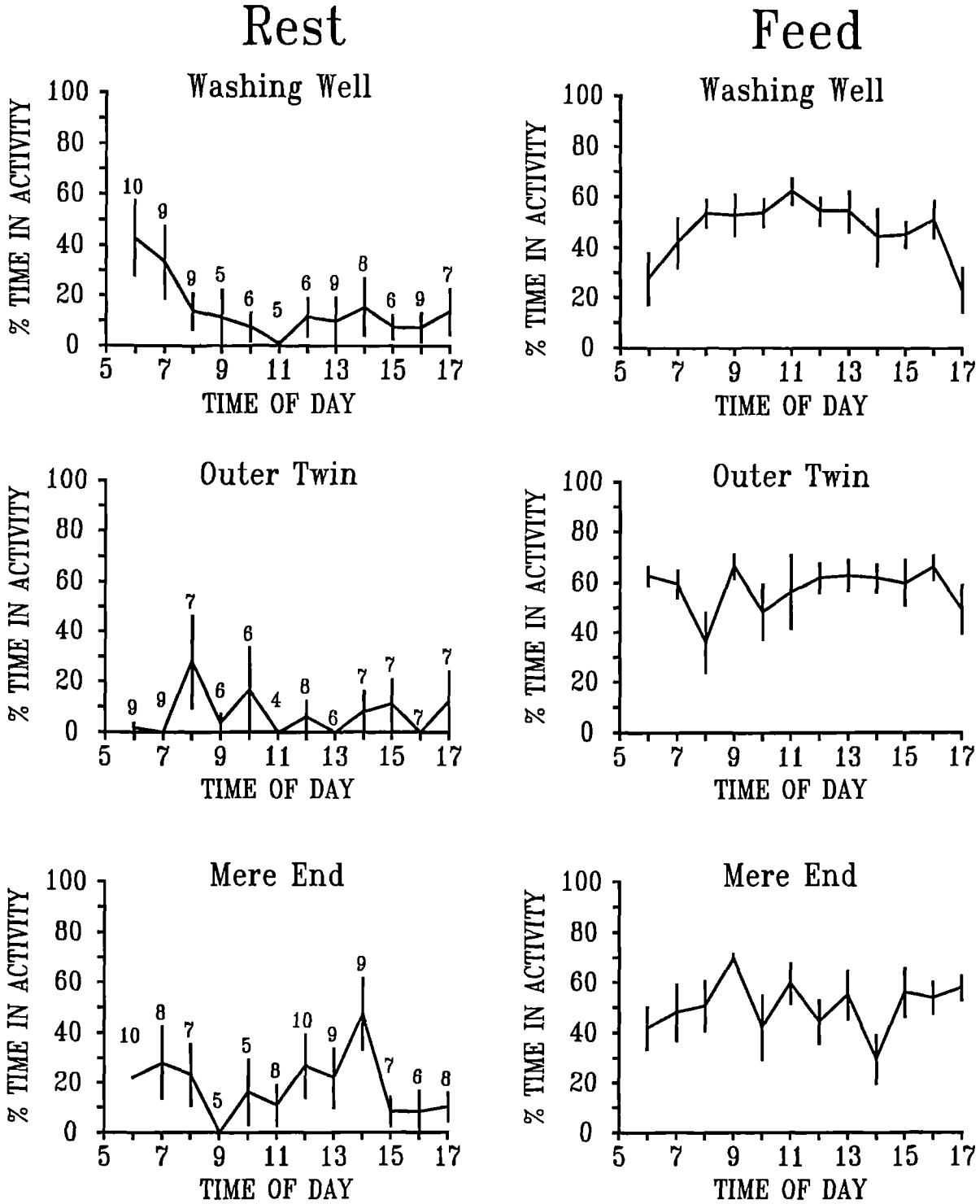

FIGURE 3.3a. Change in diurnal activity of courting male Ruddy Duck at MSWNR during the courtship period - rest and feed. Vertical bars represent ± 1 S.E.. Sample sizes are given above error bars.

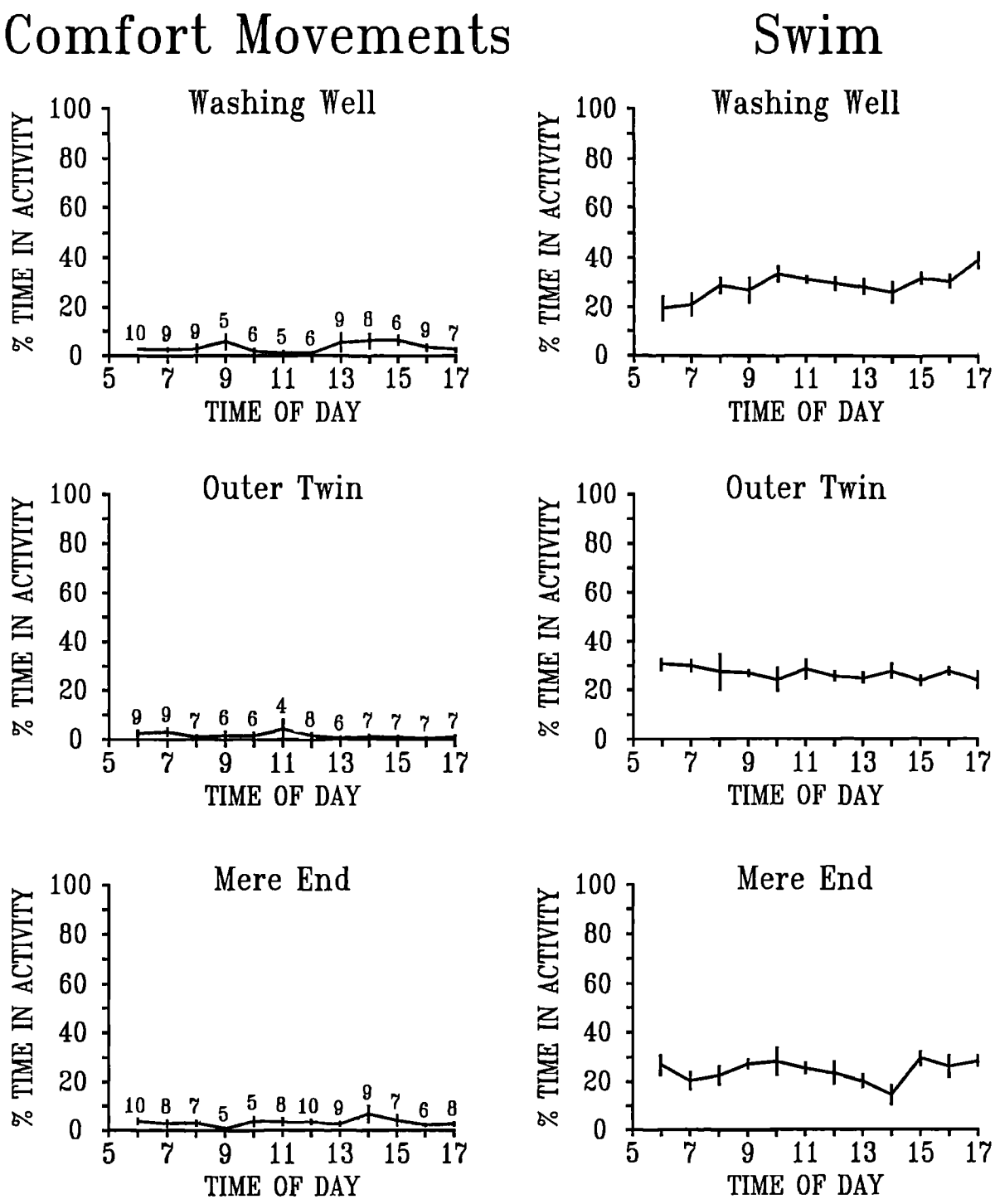

FIGURE 3.3b. Change in diurnal activity of courting male Ruddy Duck at MSWNR during the courtship period - comfort movements and swim. Vertical bars represent ± 1 S.E.. Sample sizes are given above error bars.

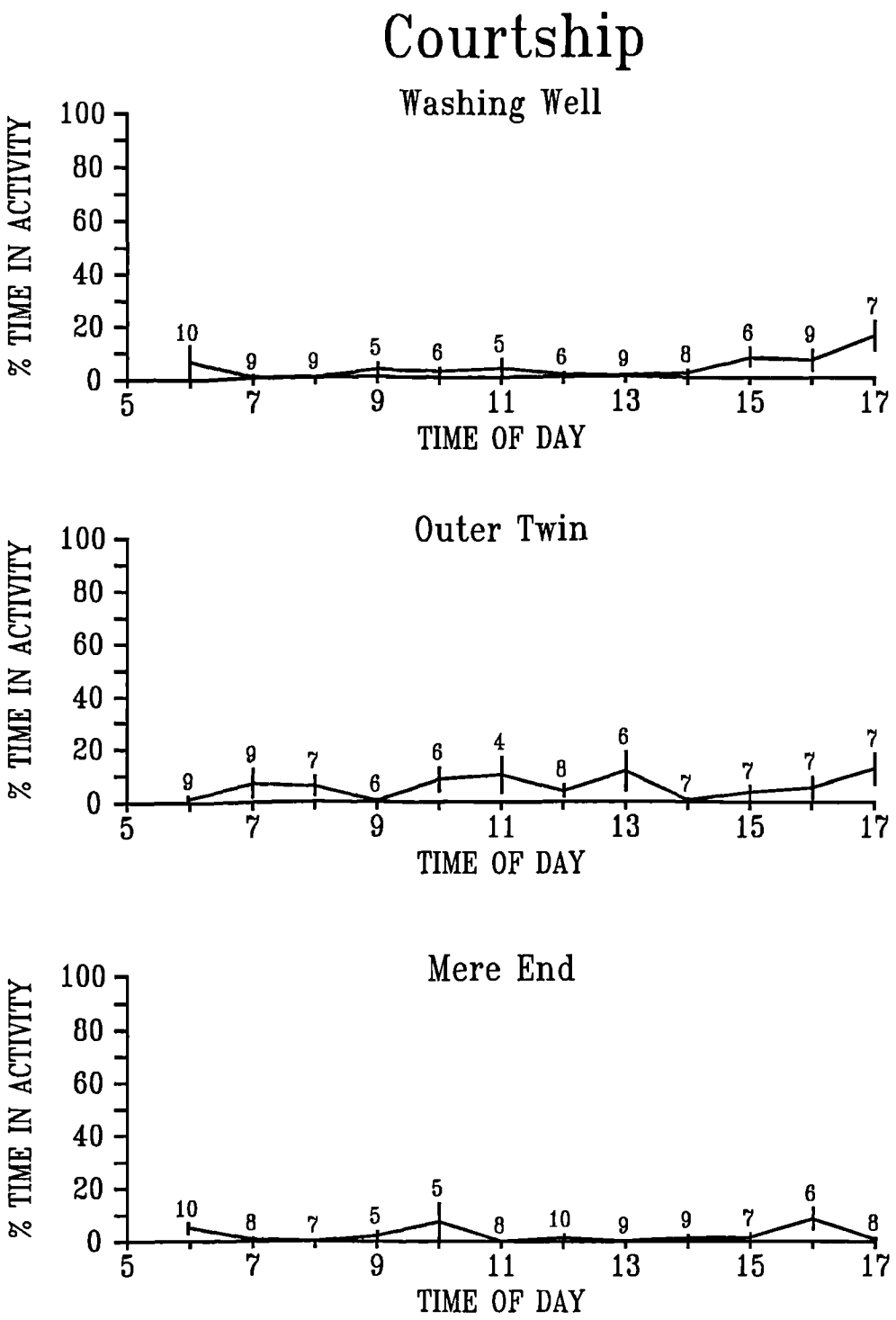

FIGURE 3.3c. Change in diurnal activity of courting male Ruddy Duck at MSWNR during the courtship period - courtship behaviour. Vertical bars represent ± 1 S.E.. Sample sizes are given above error bars.

3.4.5 Effect of Date on Behaviour

Seasonal differences in behaviour varied between lakes (Table 3.8). WW males rested significantly more and swam significantly less in early courtship period whilst ME males rested significantly less and fed significantly more during the same time. These differences were further emphasised by significant correlations with date (Table 3.7). Date was significantly negatively correlated with rest in WW males and feed in ME males whilst it was significantly positively correlated with swim in WW males and rest in ME males. The behaviour of OT males did not change with date.

3.4.6 Effect of Temperature on Behaviour

At temperatures below the median value, WW males rested significantly more and fed significantly less than at temperatures above the median (Table 3.9). These results were supported by a significant negative correlation between actual ambient temperature and rest and a significant positive correlation with feed (Table 3.7). WW males also showed a significant positive correlation between actual ambient temperature and swim. OT and ME males showed no change in behaviour with actual ambient temperature.

Mean daily ambient temperature and maximum daily ambient temperature were significantly negatively correlated with rest and significantly positively correlated with swim in WW males whilst OT males showed a significant positive correlation between mean daily ambient temperature and rest. ME males showed a significant negative correlation between maximum daily ambient temperature and courtship display. Overnight minimum ambient temperature and feed were significantly negatively correlated in OT males, but significantly positively correlated in WW males. OT males showed a significant positive correlation between overnight minimum ambient temperature and rest.

Tables 3.10 and 3.11, which provide a comparison of male waterfowl time budgets during the courtship period, are located and considered in section 3.5.1.

TABLE 3.8. Diurnal time budget of male Ruddy Duck on three lakes at MSWNR in early and late courtship period. For each site, means with different letters are significantly different between morning and afternoon categories (MW U-Tests, $P<0.05$).

	Washing Well				Outer Twin				Mere End			
	Early		Late		Early		Late		Early		Late	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Rest	22.97 a	5.162	9.81 b	3.389	6.16	3.710	8.11	3.454	12.31 a	5.715	23.71 b	4.034
Comfort Movements	3.86	0.733	3.24	0.852	1.94	0.486	1.71	0.416	2.51	0.577	3.85	0.636
Swim	25.46 a	1.876	30.89 b	1.300	27.65	1.560	26.32	1.183	23.67	1.792	23.86	1.414
Feed	42.81	4.008	49.94	3.195	55.84	3.591	59.47	2.885	58.91 a	4.390	45.94 b	3.188
Courtship Display	3.03	1.202	4.74	1.639	7.50	2.258	4.05	1.216	2.51	0.903	2.10	0.729
Total Time Watched (Hrs)	17.42		17.50		13.89		19.99		11.01		28.05	
No. of Observation Periods	44		45		35		48		28		64	

TABLE 3.9. Diurnal time budget of male Ruddy Duck on three lakes at MSWNR during the courtship period - effect of ambient temperature. For each site, means with different letters are significantly different between temperature categories (MW U-Tests, $P<0.05$).

	Ambient Temperature					
	< Median		Median		> Median	
	Mean	S.E.	Mean	S.E.	Mean	S.E.
Washing Well						
Rest	26.99 a	6.022	8.58	4.735	8.32 b	3.128
Comfort Movements	3.50	0.688	3.21	0.751	3.66	1.010
Swim	24.81	2.200	30.36	1.218	30.83	1.236
Feed	39.39 a	4.441	51.76	3.525	51.62 b	3.395
Courtship Display	3.77	1.909	4.04	2.105	3.98	1.247
Total Time Watched (Hrs)	14.66		3.83		16.44	
No. of Observation Periods	38		9		42	
Outer Twin						
Rest	5.97	4.154	1.13	1.126	11.47	4.585
Comfort Movements	1.23	0.326	2.34	0.841	2.12	0.576
Swim	26.80	1.463	27.90	1.654	26.49	1.676
Feed	62.28	3.240	59.16	3.813	53.16	4.049
Courtship Display	3.47	1.428	8.77	4.121	5.93	1.662
Total Time Watched (Hrs)	14.37		6.80		12.71	
No. of Observation Periods	33		16		34	
Mere End						
Rest	21.78	5.117	24.78	11.729	17.41	8.917
Comfort Movements	3.55	0.824	1.31	0.362	3.92	1.305
Swim	23.38	1.578	24.6	4.348	24.02	3.169
Feed	47.51	4.026	47.45	7.788	53.00	3.993
Courtship Display	3.47	1.114	1.26	1.063	1.20	0.558
Total Time Watched (Hrs)	17.96		3.80		17.32	
No. of Observation Periods	41		11		40	

3.5 DISCUSSION

3.5.1 Diurnal Time Budget

The predominant activity of male Ruddy Ducks during this study was feeding, whereas Siegfried (1973a) suggested that courting male Ruddy Ducks in Manitoba spent about 65% of their day loafing or sleeping. Resting/comfort movements also constituted most of the diurnal time budget of paired male Ruddy Ducks during the pre-nesting season in California whilst single males spent most of their time swimming (Gray 1980). The lack of diurnal feeding in these studies will probably be compensated for by increased nocturnal feeding, but there are many other variables, not least of all available food supply, which could cause these observed differences in diurnal activity. As the behaviour of Ruddy Ducks differs with social status and reproductive stage of the breeding season (Gray 1980), the exact timing of the study period may significantly affect the resulting time budget. In addition, the differences may be due, in part, to the small sample size of pre-nesting observations in Gray's study resulting from her need to observe both males and females throughout the breeding season and to the qualitative nature of Siegfried's work.

As in Ruddy Ducks in this study, feeding is the prevalent diurnal behaviour of most male Anatidae studied during the courtship period (Tables 3.10 and 3.11).

This is not surprising considering the high degree of mate defence and correspondingly high energy requirements which are necessary during subsequent phases of the breeding cycle. It is likely that ducks, such as Mallard and Lesser Scaup, which show low levels of diurnal feeding (Asplund 1981; Siegfried 1974) will also be feeding nocturnally. Unfortunately, many of the studies of courting male waterfowl in Tables 3.10 and 3.11 involved the collection of small amounts of data suggesting these results should be viewed with caution.

Some of the male waterfowl time budgets in Tables 3.10 and 3.11 are not directly comparable due to the use of different definitions of behaviour categories (see section 2.5.1) and breeding season terminology. In waterfowl, three different terms have been used to refer to stages of the breeding cycle before laying: spring arrival, pre-laying and pre-nesting. Spring arrival generally refers to the first stage at the breeding grounds in which birds are usually in flocks without intraspecific aggression. The pre-laying stage

TABLE 3.10. Diurnal time budgets of male diving ducks during the breeding season. a - observations from Long Point Bay, Ontario. b - observations from Mississippi River, Wisconsin. c - includes loafing. d - data collected from permanently flooded wetlands. e - includes dive pause. f - median behaviour values. g - includes social interactions. h - phase of breeding season not stated. X - behaviour not recognised.

Species	Reference	Season	Sample Size (Hrs)	Behaviour					
				Rest	Comfort Movements	Swim/ walk	Feed	Alert	Courtship Display
Canvasback - paired [a]	Lovvorn (1990)	Spring migration	2	21	15	8	43	Tr	9
Canvasback - single [a]	Lovvorn (1990)	Spring migration	33	22	15	14	33	Tr	13
Canvasback - paired [b]	Lovvorn (1990)	Spring migration	2	17	10	19	43	1	7
Canvasback - single [b]	Lovvorn (1990)	Spring migration	23	19	13	26	34	Tr	6
Lesser Scaup - paired	Siegfried (1974)	Pre-laying	179	42 [c]	2	20	35	X	X
Lesser Scaup - single	Siegfried (1974)	Pre-laying		67 [c]	1	17	15	X	X
Lesser Scaup [d]	Gammonley and Heitmeyer (1990)	Spring migration 1986	c5	10 [c]	11	23	44 [e]	Tr	12
Lesser Scaup [d]	Gammonley and Heitmeyer (1990)	Spring migration 1987	c5	32 [c]	8	11	42 [e]	Tr	7
Bufflehead [d]	Gammonley and Heitmeyer (1990)	Spring migration	c10	4 [c]	8	12	70 [e]	Tr	6
White-winged Scoter	Brown and Fredrickson (1987)	Pre-laying	98	17	12	30	36	4	1
Ruddy Duck	This study	Spring arrival and pre-laying	108	15	3	26	51	Tr	4
Ruddy Duck - paired	Gray (1980) [f]	Spring arrival and pre-laying	9	48 [c]		9	16	X	2 [g]
Ruddy Duck - single	Gray (1980) [f]		7	18 [c]		51	26	X	3 [g]
Maccoa Duck - paired	Siegfried *et al* (1976a)	Breeding season [h]	89	29	10	19	29	X	13

TABLE 3.11. Diurnal time budgets of paired male dabbling ducks during the early breeding season. a - Free-ranging pinioned birds. b - includes loafing. X - behaviour not recognised.

Species	Reference	Season	Sample Size (Hrs)	Behaviour					
				Rest	Comfort Movements	Swim/ walk	Feed	Alert	Courtship Display
Mandarin	Bruggers and Jackson (1977) [a]	Pre-laying	15	33	10	34	21	0	X
Shoveler	Afton (1979)	Spring arrival	12	19 [b]	6	3	64	7	X
Shoveler	from Afton (1979)	Pre-laying	18	22 [b]	12	6	54	5	X
Mallard - lake 1	Asplund (1981)	Spring arrival, pre-laying and laying	11	23	9	48	16	4	X
Mallard - lake 2	Asplund (1981)		3	55	4	39	14	2	X
Black Duck	Seymour and Titman (1978)	Spring arrival	257	7 [b]		X	84	X	X
Black Duck	Seymour and Titman (1978)	Pre-laying	79	18 [b]		X	75	X	X
Gadwall	Dwyer (1975)	Spring arrival	13	8	9	9	72	1	X
Gadwall	Dwyer (1975)	Pre-laying	35	14	12	8	54	11	X

has been defined in two ways: behaviourally and physiologically. Firstly, as a period characterised by increased intraspecific intolerance between birds (e.g Dwyer 1975) and, secondly, as the duration of ovarian development in females (e.g. Tome 1981). The pre-nesting stage referred to by some authors (e.g Dwyer 1975; Gray 1980) corresponds roughly to the pre-laying phase.

If the pre-laying stage is defined as the duration of ovarian development in females then most of the data in this study were collected in the spring arrival period before the onset of the pre-laying period in the first female Ruddy Duck to nest. The first brood at MSWNR in 1989 was observed on 25 May. Assuming an ovary development period of 11 days (Gray 1980), a mean clutch size in active nests of 7 eggs (B. Hughes unpubl. data) and a laying rate of one egg per day (Palmer 1976), an incubation period of 23 days and that ducklings remain in the nest for approximately 24 hours after hatching (Palmer 1976) then the beginning of the pre-laying period in the first Ruddy Duck to nest at MSWNR in 1989 can be estimated as 13 April, six days before the end of the study period.

Although the overall selection pressures will be basically similar for all breeding male anatids, that is, the need to secure a mate and ensure individual fertilisation of that female's eggs, there is considerable variation in diurnal time budgets of male ducks during the courtship period within and between species. Interspecific differences may result from intrinsic factors, such as body size, preferred food and feeding mechanisms, breeding strategy, age-ratio and sex-ratio. Other factors will affect time budgets intra- and interspecifically on a study-by-study basis, such as date of observation (Dwyer 1975), year and site (Gammonley and Heitmeyer 1990), weather conditions (Danell and Sjöberg 1982), latitude, time of observation and observation sampling method. Furthermore, this study has emphasised the need for construction of waterfowl time budgets not only on a site-by-site basis, but actually for individual lakes within a specific site, as the time budgets of courting male Ruddy Ducks at MSWNR differed significantly between the individual lakes.

The higher amount of courtship activity and the lower amount of resting on the Outer Twin can probably be explained by the fact that higher numbers of birds congregated on this lake stimulating higher levels of courtship display. It is possible that this higher level

of energetically expensive activity may have necessitated a higher amount of feeding.

Variables which have a significant effect on the time budgets of breeding male waterfowl, such as pairing status (Lovvorn 1990), date, weather conditions and year may affect the behaviour of birds on different lakes within a site in a similar fashion. However, there are a number of site-specific variables operating at the microhabitat level which may have a direct bearing on the behaviour of waterfowl on a lake-by-lake basis. These include microclimatic conditions, which will be related to habitat characteristics such as the degree of surrounding tree cover, the extent of emergent vegetation, the extent of open water and the stability of the water level. The presence/absence and abundance of conspecifics (see section 3.5.3) and other species, both potential predators and/or potential competitors, may also modify the observed time budget of waterfowl on a lake-by-lake basis.

3.5.2 Effect of Paired Status on Behaviour

On two of the three lakes, the behaviour of paired and single males did not differ significantly, but on the Mere End paired males rested significantly more and fed significantly less than single males. After the day the first paired bird was observed, paired and single males showed no significant differences in behaviour, but this was probably a reflection of the smaller sample size for each site and the inherent variability in the data, as paired males on the Mere End still rested more and fed less than single males.

Paired and single male Ruddy Ducks during the pre-nesting season in Manitoba showed similar significant differences in behaviour as the birds on the Mere End (Gray 1980). This situation can be explained as follows. Ruddy Ducks tend to breed later than other diving ducks (Miller and Collins 1954), therefore, at the time of pair formation, males will have had adequate time to acquire the energy reserves necessary for breeding, mainly the defence of their mate. Once paired, males then conserve energy by resting while their mate continues to feed. In fact, paired males actually assumed pseudo-sleeping postures and remained close to their mates at this time. In common with all species of stifftail, a dominance hierarchy of male Ruddy Ducks is established on the breeding grounds during courtship. Dominant males are first to acquire mates while less dominant single males continue to feed and strive to improve their condition in order to obtain a mate, either by

attracting a single bird or by usurping an already paired male (c.f. Gray 1980). No nocturnal observations were made, therefore it is possible that the imbalance in the level of feeding between paired and single males might be redressed at night. Paired male Mallard during the laying period also fed less than single males (Asplund 1981) whilst male Ring-necked Duck reduce feeding activity and expend fat reserves while attending pre-laying/laying females (Hohman 1985).

In contrast, paired male Lesser Scaup during the pre-laying period rested less and fed more than single males (Siegfried 1974). Siegfried suggested this was because feeding in paired males was more leisurely and more often interrupted than in single males. Lovvorn (1990) reported that paired male Canvasback tended to feed more and swim less than single males during spring migration probably because widespread defence of feeding sites by dominant paired males excluded single birds. Gray (1980) also found that single male Ruddy Ducks swam significantly more than paired males and suggested that this was caused by increased effort in locating females. The fact that pairing status did not have any effect on the amount of swimming activity at MSWNR is probably a reflection of the difference in the size of the two study sites: Gray's study site was considerably larger than the lakes at MSWNR, hence the location of females was more difficult. Increased swimming by single male dabbling ducks, such as Gadwall, Mottled Duck and Green-winged Teal, during winter is thought to result from birds actively seeking and courting females, avoiding dominant paired birds and increasing food-seeking activity due to the domination of preferred feeding sites by paired birds (Paulus 1984, 1988a; Rave and Baldasarre 1989).

On all three lakes at MSWNR, single males displayed more than paired males although the differences were not significant. In California, although the level of courtship display was similar, single male Ruddy Ducks displayed at a consistently higher rate than paired males (Gray 1980). Single male Canvasback on spring migration also displayed more than paired males (Lovvorn 1990). Similarly, single male Mallard and Green-winged Teal (Turnbull and Baldasarre 1987; Rave and Baldasarre 1989) in winter displayed significantly more than paired birds, therefore it appears that single male anatids invest more time and energy than paired males in courtship display in an attempt to attract a mate.

Pair formation and corresponding peaks in courtship display in dabbling ducks occurs on the wintering grounds, hence the notable absence of courtship display in their spring time budgets (Tables 3.10 and 3.11). Most freshwater diving ducks pair either on the breeding grounds or during spring migration and therefore show relatively higher levels of courtship display at this time of year. The low level of diurnal courtship display in Ruddy Ducks is augmented by active courtship during the hours of darkness, both in the wild and in captivity (B. Hughes unpubl. data).

3.5.3 Effect of the Presence of Other Male and Female Ruddy Duck on Behaviour

Because of the excess of males at MSWNR, there was insufficient data in the "other males absent" category to draw meaningful conclusions from the results from the Washing Well and Outer Twin. On the Mere End, there was no significant difference in the behaviour of courting males with and without other males present. The absence of courtship display in the males absent category in WW and OT males is probably a result of the small sample size due to the relatively short duration of bouts of this behaviour. Male presence was scored in a one-zero fashion when in fact it would have been more useful to actually note the number of other male Ruddy Ducks present. Higher levels of courtship activity in males appeared to be stimulated by higher numbers of other males present, but it was not possible to test this hypothesis.

On the Washing Well, there was no difference in the behaviour of courting males with and without the presence of females, but on the Mere End, males appeared to spend more time resting and less time feeding in the presence of females. However, a correlation between pairing status, female presence and date for the observations of ME males and the small sample size and non-interactive nature of the non-parametric analysis employed by necessity severely limited further interpretation. There was a bias for earlier observations in the study period to involve single males without females present, therefore it was difficult to determine which was the causative factor in the change in behaviour of ME males. In the only other study of the effect of female presence on male behaviour in anatids, Dwyer (1975) found that paired male Gadwall tended to spend less time feeding when their mate was present.

Most ducks do not display in the absence of females, so a higher amount of courtship

display might be expected with female Ruddy Ducks present than when they were absent. However, the level of courtship display shown by courting male Ruddy Ducks was actually lower in the presence of females. This will be caused by the tendency of male Ruddy Ducks to display in situations without females present, such as in groups of displaying males or in response to a disturbance or the presence of a predator. Male Ruddy Ducks in California also displayed alone without any apparent stimulus (Gray 1980).

3.5.4 Effect of Time of Day on Behaviour

Trends in male activity with time of day were generally inconsistent between sites. Male behaviour in the morning and afternoon was similar, save for higher levels of courtship display towards evening in WW males. The decrease in resting and increase in swimming with time of day in WW males is probably related to the accompanying increase in courtship activity. This increase in courtship activity in the evening also occurs in captive stifftails (Carbonell 1983; B. Hughes unpubl. data). Crepuscular peaks in courtship display have also been observed in Mottled Duck (Paulus 1988a) whilst Green-winged Teal and Gadwall displayed most in early morning (Quinlan and Baldasarre 1984; Paulus 1984).

Ruddy Ducks, unlike other ducks such as Mandarin *Aix galericulata* (Bruggers and Jackson 1977), do not show crepuscular patterns of feeding activity with noticeably inactive periods around midday. This is because, during the pre-nesting period, they usually show a cyclical pattern of behaviour, consisting of alternating bouts of feeding, preening and resting (Siegfried 1973a). As this cyclical activity pattern varies in timing and duration, there is no predictable pattern of behaviour in relation to time of day.

3.5.5 Effect of Date on Behaviour

Date did not have any predictable effect on the behaviour of courting male Ruddy Ducks on the three lakes at MSWNR. WW males rested significantly more in early season whilst the opposite was true for ME males. This result for ME males was confused by a correlation between the effects of date, pairing status and female presence, however, the higher level of feeding in early season is comparable to the findings of Dwyer (1975) and

Afton (1979) who showed a decrease in the level of feeding behaviour by male Gadwall and male Shoveler as the breeding season progressed. Both paired and single male North American Black Ducks also showed a progressive decline in feeding activity during the breeding season (Seymour and Titman 1978, 1979). Afton (1979) argued that the decline in feeding was caused, in part, by an increase in predator monitoring and territorial defence behaviours whilst Dwyer (1975) suggested it was due to higher temperatures providing an increased food supply. The former hypothesis may well be involved in explaining the decrease in feeding behaviour of ME males as the season progressed, but it is unlikely that the latter is important (see section 3.5.6). Increased feeding by male ducks in early breeding season is necessary to amass energy reserves in readiness for the increased level of mate defence which they must maintain during the pre-laying and laying periods.

3.5.6 Effect of Temperature on Behaviour

Actual ambient temperature only had a significant effect on the behaviour of WW males, which rested less and swam and fed more at higher temperatures. Few other studies have assessed the effect of temperature on the behaviour of male ducks during the courtship period. Quinlan and Baldasarre (1984) found that in February and March Green-winged Teal also showed a significant negative correlation between temperature and rest and a significant positive correlation between temperature and swim. They explained this in terms of higher resting, and hence higher energy conservation, at lower temperatures. In contrast, Paulus (1984) found that non-breeding Gadwalls spent more time resting and less time feeding at higher temperatures and explained this in terms of warmer temperatures reducing energetic needs. Non-breeding Mottled Ducks also fed more at lower temperatures (Paulus 1988a).

Dwyer (1975) suggested that higher ambient temperatures may result in an increased food supply for waterfowl and a subsequently lower level of feeding behaviour. More feeding by WW males at higher temperatures may suggest that this theory cannot be applied to male Ruddy Ducks at MSWNR, but since the theory depends on the activity and availability of prey species, which were not studied at MSWNR, it is impossible to speculate further. Besides, the activity and availability of different species of chironomids, the preferred food of Ruddy Ducks, differs between species depending on

temperature, photoperiod and light intensity (Luferov 1971; Kureck 1980; Wrubleski and Ross 1989), therefore the exact food of the birds would also need to be established. Since Ruddy Ducks may prefer to feed nocturnally during the courtship period, the inclusion of nocturnal time budget data would also be necessary.

It might be expected that WW males would be most likely to show the most significant changes in activity with temperature as they experienced the widest range of temperatures. However, as the changes in activity with temperature were not consistent between lake systems, it appears that temperature has little predictable effect on the behaviour of courting male Ruddy Ducks at the temperatures experienced. In addition, attempting to explain the complex microclimatic habitat of an active waterbird through simple ambient temperature readings taken some distance away has obvious drawbacks.

In OT males, overnight minimum temperature was significantly negatively correlated with feed and significantly positively correlated with rest. Although this would be consistent with the hypothesis that warmer overnight temperatures facilitate higher levels of preferred nocturnal feeding, the correlation between overnight minimum temperature and feeding was reversed in WW males thus again suggesting that there was no predictable relationship between temperature and diurnal activity.

3.6 CONCLUSIONS

The behaviour of male Anatidae during the early breeding season is affected by many factors. Pairing status, time of day, date, year, weather conditions, habitat characteristics and the presence/absence and abundance of conspecifics and other species may all have a significant effect on behaviour. Such a high number of variables all operating at different levels and affecting different species in different ways emphasise the need for the construction of time budgets on a site-by-site or even lake-by-lake basis. All have been shown to have a significant effect on male behaviour, yet it is difficult to study the interaction between individual variables given the inherent problems in the analysis of time budget data.

This study provides a general overview of the behaviour of male Ruddy Ducks during the courtship period, yet it raises further questions for the collection and analysis of time

budget data.

1. Is it preferable to collect data on as many birds as possible within a complex of lakes if the possibility exists that their behaviour may differ significantly between lakes or is it acceptable to concentrate on obtaining more data on a smaller number of birds at a given lake?

2. Can meaningful conclusions be drawn from very basic analyses of climatic variables measured at a macroscopic level when many climatic variables actually operate at a microclimatic level and are subject to many sources of variation?

3. Given the limited non-interactive nature of non-parametric statistical analysis of non-normally distributed time budget data and given the fact that factors affecting waterbird behaviour are generally interactive, would it be preferable to analyse time budget data using multivariate parametric statistics in the knowledge that the assumption of normality is violated?

In the past, behavioural ecologists have made these decisions individually as there is no standard reference including detailed guidelines for the collection and analysis of time budget data. From the examination of time budget studies during the courtship period and at other times of the year, the need for a standardised system of time budget data collection and analysis is wholly apparent. Given the inherent variability of time budget studies and the many factors which can affect results, it seems necessary to eliminate any controllable sources of variation. A standard reference on the subject containing standard behavioural categories, standard terminology for use during all phases of the yearly cycle and set guidelines for statistical analysis would be a first step in achieving this aim.

CHAPTER FOUR.

DIURNAL TIME BUDGET OF BROOD FEMALE RUDDY DUCKS AT MERE SANDS WOOD NATURE RESERVE, LANCASHIRE.

4.1 INTRODUCTION

Studies of the activities of breeding Anatidae have often excluded consideration of the behaviour of the brood female and have been carried out from the time of arrival on the breeding grounds through incubation (Mandarin Duck - Bruggers and Jackson 1977; Gadwall - Dwyer 1975; North American Black Duck - Seymour and Titman 1978, 1979; Shoveler - Afton 1979; Ruddy Duck - Tome 1981, 1991). In recent years, brood female behaviour has received increasing attention, with work carried out on Mallard (Asplund 1981), Pintail (Rushforth Guinn and Batt 1985), Lesser Scaup (Afton 1983, 1984), Harlequin Duck *Histrionicus histrionicus* (Edwards and Hughes 1986), Velvet Scoter *Melanitta fusca fusca* (Kurilovich and Tarkhanova 1986), White-winged Scoter *Melanitta fusca deglandi* (Brown and Fredrickson 1987), Goldeneye (Kurilovich and Tarkhanova 1986) and Maccoa Duck (Siegfried *et al* 1976a). There have also been a number of studies of the activity of brood female geese (Harwood 1977; Ebbinge and Ebbinge-Dallmeijer 1977; Lazarus and Inglis 1978; Giroux *et al* 1986; Eberhardt *et al* 1989).

Despite the attention which Ruddy Ducks have received during the breeding season, only Gray (1980) has included brood female behaviour in her work. Joyner (1975) and Siegfried (1977) noted the increased independence of ducklings with increasing age, but did not consider the change in the behaviour of the accompanying female.

As ducklings mature, a change in the behaviour of brood females may be expected concerning the level of parental care and its conflict with the females' need to replenish nutrient reserves depleted during incubation. In accordance with parental investment theory, parental investment should decline at a stage of offspring development when the cost of care by the parent becomes greater than the benefit to the offspring (Trivers 1972). Increased feeding behaviour by brood females may also be expected immediately following hatching to compensate for endogenous reserves metabolised during incubation.

This study aimed to quantify the behaviour of brood female Ruddy Ducks at MSWNR and investigate changes in behaviour with increasing brood age, time of day and temperature.

4.2 STUDY AREA

This study was performed at MSWNR (see section 3.2).

4.3 METHODS

4.3.1 Diurnal Time Budget

Diurnal time budget data were collected between 2 June and 1 July 1988 and between 15 June and 29 July 1989. For the first 16 study days during 1988, daylight hours between 0600h and 1800h were sampled once in a unit of two days, but for the final eight study days in 1988 and all days in 1989, all daylight hours, from 0400h until 2200h, were sampled once in a unit of three days. During most of the study, there was only one brood present at any one time. If there were two broods present, however, then the first was observed for a three day period, in order to sample all daylight hours, then the following three days were spent observing the second brood. Observations ceased at the breakdown of the hen-brood bond. Methods of observation were identical to those used in the previous time budget studies.

Observations of brood females were made from permanent hides on the Washing Well and Extraction and from temporary canvas hides on the Mere End, Heath Lake and End Lake (Fig. 4.1). Brood age and size was noted for each female under observation along with ambient temperature. Maximum daily and overnight minimum ambient temperature were recorded on a daily basis. Surveys for new broods were performed daily on the whole lake complex. Broods were assumed to be one day old when first observed since they spend their first 12-24 hours in the nest (Palmer 1976; Siegfried 1977; H. Hays unpubl. notes).

A summary of the behaviours exhibited by the brood female Ruddy Ducks at MSWNR is given in Table 4.1. Many of these behaviours were similar to those recorded in Chapters Two and Three with the following additions or modifications.

FEED - Also included:-

Feed-land - Feeding directly from the surface of the land.

NEST MAINTENANCE - Maintenance of nest platform (used for loafing purposes).

TABLE 4.1. Behaviours exhibited by brood female Ruddy Duck at MSWNR. L denotes behaviour performed on land.

REST	- Sleep (L)	
	- Pseudosleep (L)	
COMFORT MOVEMENTS	- Preen (L)	
	- Roll-cheeks-on-back (L)	
	- Rest-preen	- Foot-shake (L)
		- Tail-shake (L)
	- Scratch (L)	
	- Stretch (L)	
	- Bill-dip (L)	
	- Bathe	
	- Wing-shiver (L)	
	- Wing-flap	
	- Minor comfort activities	- Yawn (L)
		- Foot-shake (L)
		- Tail-shake (L)
		- Head-shake (L)
SWIM	- Loaf	
	- Locomotion	
	- Inter-dive interval	
ALERT	- Head-up (L)	
	- Extreme head-up (L)	
	- Extreme head-up-tail-up	
	- Head bob (L)	
	- Head flick	
FEED	- Dive	
	- Dabble (L)	
	- Drink	
	- Head-under	
	- Feed-land (L)	
NEST MAINTENANCE (L)		
LAND (L)		
PARENTAL CARE	- Lead (L)	
	- Follow (L)	
	- Social interaction	
	- Intraspecific	- initiated by study bird (L)
		- initiated by another bird
	- Interspecific	- initiated by study bird (L)
		- initiated by other species
	- Unknown species (L)	
	- Avoidance	
FLY		
SKEETER		

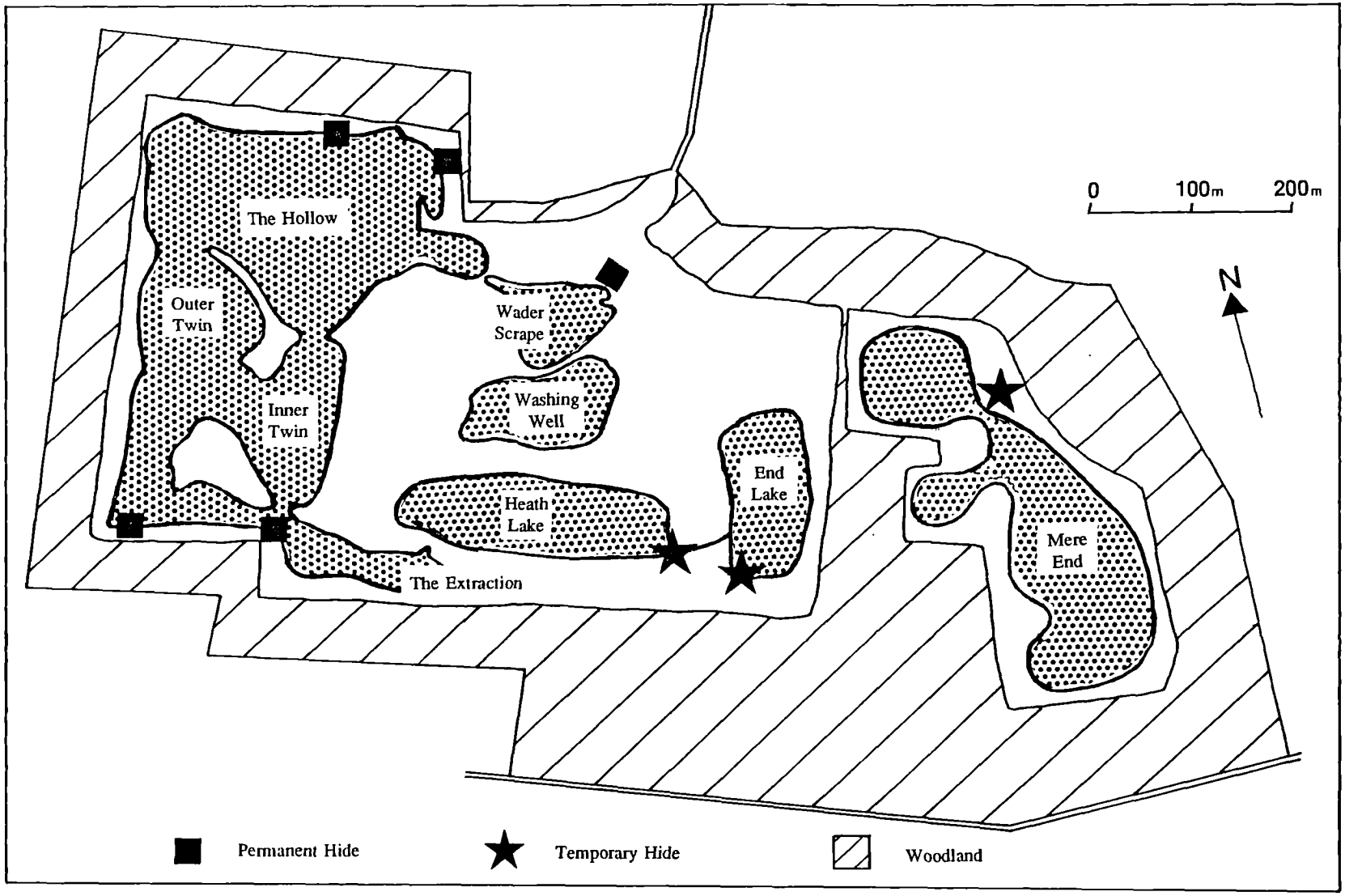

FIGURE 4.1. Map of MSWNR showing sites of observation during the brood female time budget.

PARENTAL CARE - Behaviours which can be directly related to brood care. This category included the following activities:-

Lead - Leading the brood to preferred sites of activity, that is, when the female was swimming with more than half of the brood behind her (Rushforth Guinn and Batt 1985).

Follow - Following the brood to preferred sites of activity, that is, when the female was swimming with more than half of the brood in front of her.

Social Interaction - Both intra- and interspecific interactions. This behaviour included an "unknown" category, in which the other species involved in the interaction could not be determined, and an avoidance category as in Chapter Two (see section 2.3.1). Social interactions are analysed in detail in Chapter Five.

ALERT - Often accompanied by an erection of the ear tufts by the brood female. This posture elicited a grouping response in the brood, especially with younger ducklings. Alert behaviour included the same head-up, extreme head-up, extreme head-up-tail-up and head bob postures described in Chapter Two plus one extra behaviour characteristic of females in the highest state of alert:-

Head Flick - While in extreme head-up posture the head is flicked quickly from side to side. A similar behaviour occurs as pre-flight signalling (Palmer 1976; H. Hays unpubl. notes) which is also common in *Aythya* species, such as Tufted Duck and Scaup.

This gives a total of 41 behaviours which were amalgamated into ten mutually exclusive categories for analysis. Twenty six of the behaviours were performed on both land and water, but for the purpose of the analysis land and water categories were combined. Although the behaviour of brood female Ruddy Ducks is described in this chapter, the results will also provide a rough indication of duckling activity because of their habit of copying the behaviour of the brood female. This becomes less frequent with increasing duckling age due to their increasing independence.

4.3.2 Data Analysis

As in Chapter Two, the number of records of each behaviour were expressed as a percentage of the total records for each observation period. Any mutually exclusive behaviour category which constituted ≥5% of the total diurnal time budget of any of the brood females was defined as a major activity and selected for further analysis. Analysis of the behaviours concerned with parental care (lead, follow and social interaction) involved performing statistical tests on behaviours which constituted <5% of the total time budget of the individual brood females. The small sample size resulting from this condition and the associated high probability of obtaining spurious results is realised.

To analyse the effect of brood age on the behaviour of the brood females another variable, ageclass, was included in the data set. This variable simply depended on the age of the ducklings in the brood and not on their body size or plumage development. Four ageclasses were recognised:-

Ageclass 1. Brood age 1-7 days.
Ageclass 2. Brood age 8-14 days.
Ageclass 3. Brood age 15-21 days.
Ageclass 4. Brood age ≥22 days.

Ageclasses per brood with less than ten observation periods were excluded from the analysis.

Four temperature variables were included in the analysis: actual ambient temperature, mean daily ambient temperature, maximum daily ambient temperature and overnight minimum ambient temperature. The amount of time two of the brood females spent out of sight was analysed separately as part of this analysis.

The data were analysed using the SYSTAT computer package (Wilkinson 1987). Data from broods which did not survive to fledging, data when birds were out of sight and observation periods less than 10 minutes long were excluded from the analysis. Sample sizes in the statistical procedures refer to the number of observation periods per brood female and all other statistical methods were similar to those used in Chapter Two.

4.4 RESULTS

4.4.1 Diurnal Time Budget

In both 1988 and 1989 there were potentially ten breeding pairs of Ruddy Ducks present at MSWNR, yet only eight broods in total (four in 1988, four in 1989) hatched successfully (Table 4.2). Of those eight broods, only four (two in 1988, two in 1989) survived to fledging and are included in the analysis. The females from these four broods are referred to as females 1, 2, 3 and 4, but this numbering system has no implications for brood age, size or date of hatching.

Broods were observed on all nine distinct lake areas with two of the broods actually moving between lakes. One brood movement (brood 1) occurred between the End/Heath Lake complex and the Washing Well, after a brood female Goldeneye had killed one of the ducklings from the brood. This involved a brood of four four-day old ducklings making an overland journey of approximately 10m. The other movement occurred overnight on 16 June 1989 when Brood 4 (five ducklings aged four days old) moved from the Extraction to the Washing Well, a minimum overland distance of about 200m.

The study period for both years consisted of 54 study days (24 in 1988, 30 in 1989). A total of 318 hours of observation (138 hours in 1988, 180 hours in 1989) provided only 128.81 hours of usable data (48.40 hours in 1988, 80.41 hours in 1989). This lack of data was mainly due to the poor breeding success of Ruddy Ducks at MSWNR in both study years combined with their habit of remaining out of sight in lakeside vegetation. The data for brood female 2 were collected between 0600h and 1800h and for females 3 and 4 between 0400h and 2200h. The first eight days of observations for female 1 were performed under the former observation regime and the following seven days under the latter. The breakdown of the hen-brood bond occurred at 22, 17, 20 and 22 days of duckling age in females 1, 2, 3 and 4, respectively.

Non-parametric statistics were used in the analysis as examination of probability plots for the major behaviours showed the data to be non-normally distributed even after angular transformations had been performed. Although alert behaviour was undoubtedly an important component of parental care, it was analysed separately as the level of alert varied widely between females as it was subject to influence by external factors, such as the presence/absence and behaviour of other species and the physical features of

TABLE 4.2. Ruddy Duck broods at MSWNR during the summers of 1988 and 1989. a - figures in parentheses refer to original brood size while under observation.

Brood	Year	Hatch Date	Orig. Size	Date	Age (Days)	Size [a]	No. Fledged	Lake	Notes
				During Observation					
1	88	8/6	5	12-30/6	4-22	4 (5)	4	End/Heath Lake and Washing Well	Brood moved (12/6) after Goldeneye killed duckling
2	88	27/5	7	2-13/6	6-17	7	7	Washing Well	
Not included	88	31/5	2	4-5/6	4-5	1	0	End Lake	Remaining duckling probably killed by female Goldeneye
Not observed	88	18/6	6	-	-	-	0	Mere End	Brood last seen 21/6 - fate unknown
Not observed	89	25/5	5	-	-	-	0	Extraction	Brood seen by only one observer - fate unknown
3	89	9/7	5	16-29/7	7-20	2	2	Washing Well	Three ducklings died before observations started
4	89	12/6	5	15/6-4/7	3-22	5	5	Extraction and Washing Well	Brood moved 16/6
Not included	89	27/6	3	29/6-1/7	2-4	1 (2)	0	Mere End	Brood died in bad weather

the surrounding habitat.

Resting (20.54 ± 1.728%), swimming (35.05 ± 0.968%) and feeding (28.85 ± 1.316%) constituted most of the brood females' diurnal time budget (Table 4.3). Comfort movements (5.15 ± 0.444%), alert (4.89 ± 0.454%) and parental care (4.82 ± 0.439%) were the other major behaviours. Minor behaviour categories were fly, skeeter and land. Swimming and feeding were the major behaviour categories in all four brood females. Nest maintenance does not appear in the results as the brood female which showed this behaviour lost her brood to the effects of bad weather within four days of hatching.

The females differed significantly in all of their major behaviours (MW U-Tests, $p<0.05$) except comfort movements (Table 4.3) and were therefore treated separately in further analyses. Brood female 2 spent significantly less time resting than the other females whilst female 4 spent significantly less time swimming than female 3. Females 2 and 4 fed significantly more than females 1 and 3. Brood female 4 exhibited significantly less alert behaviour than the other females whilst females 3 and 4 spent significantly less time in parental care activities than females 1 and 2.

The females also showed significant differences in the individual parental care behaviours (Table 4.4). Females 1 and 2 were involved in a significantly higher amount of social interaction than females 3 and 4. Female 2 led her brood significantly more than the other females whilst female 1 led her brood significantly more than female 3. Females 3 and 4 followed their broods significantly less than female 2.

All brood females spent in excess of 97.5% of their time on water while behaviours commonly performed on land included resting, comfort movements, alert, lead and follow. Brood female 4 spent significantly more time on water than the other three females.

Table 4.5 provides a comparison of the time budgets of brood female waterfowl from the available literature. Unfortunately, corresponding figures for some behaviours are not directly comparable due to the variation in definition of those behaviours between studies. For example, the resting category for Ruddy Ducks in Gray (1980) included loafing, preening and sleeping, whereas it only refers to sleeping in this study. There is the added complication that some authors did not recognise certain activities. Gray (1980) and

TABLE 4.3. Diurnal time budget (percent time in activity) of brood female Ruddy Duck at MSWNR. Means with different letters are significantly different between females (MW U-Tests, $p<0.05$).

	Female 1 Size 4 (5)		**Female 2** Size 7		**Female 3** Size 2		**Female 4** Size 5		**All Females**	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Major Behaviours										
Rest	21.48 a	3.741	10.10 b	3.095	22.37 a	3.100	23.85 a	3.429	20.54	1.728
Comfort Movements	5.68	0.892	5.18	1.503	5.88	0.786	4.00	0.619	5.15	0.444
Swim	35.15 ab	2.063	34.23 ab	1.786	40.07 a	2.029	30.31 b	1.514	35.05	0.968
Feed	24.12 a	2.453	31.57 b	2.453	23.79 a	2.354	35.97 b	2.655	28.85	1.316
Alert	4.68 a	0.804	8.96 a	1.895	5.25 a	0.694	2.39 b	0.388	4.89	0.454
Parental Care	7.72 a	1.191	9.30 a	1.335	1.91 b	0.247	3.13 b	0.667	4.82	0.439
Minor Behaviours										
Fly	0	-	0	-	0.03	0.025	0	-	0.01	0.008
Skeeter	0	-	0.01	0.01	0	-	0	-	0	-
Land	1.17	0.282	0.65	0.359	0.70	0.191	0.34	0.110	0.69	0.111
% Time spent on Water	97.57 a	0.531	98.21 a	0.671	98.06 a	0.574	99.11 b	0.301	98.29	0.258
% Time spent on Land	2.43	0.531	1.79	0.671	1.94	0.574	0.89	0.301	1.71	0.258
Total time watched (Hrs)	27.76		20.64		42.95		37.46		128.81	
No. of observation periods	71		54		98		96		319	

TABLE 4.4. Diurnal time budget (percent time in activity) of brood female Ruddy Duck at MSWNR - parental care. Means with different letters are significantly different (MW U-Tests, $p<0.05$) between females.

	Female 1 Size 4 (5)		**Female 2** Size 7		**Female 3** Size 2		**Female 4** Size 5		**All Females**	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Alert	4.68 a	0.804	8.96 a	1.895	5.25 a	0.694	2.39 b	0.388	4.89	0.454
Parental Care	7.72 a	1.191	9.30 a	1.335	1.91 b	0.247	3.13 b	0.667	4.82	0.439
- Social Interaction	2.68 a	0.621	1.94 a	0.449	0.68 b	0.129	0.80 b	0.153	1.37	0.174
- Lead	3.24 a	0.711	6.14 b	1.049	0.84 c	0.154	1.76 ac	0.561	2.55	0.312
- Follow	1.80 ab	0.469	1.22 a	0.267	0.39 b	0.069	0.58 b	0.113	0.90	0.124

TABLE 4.5. Diurnal time budgets (percent time in activity) of brood female waterfowl. a - figures recalculated excluding "In Reeds" behaviour in which birds were out of sight. b - includes loafing. Females assumed to be resting during the hours of darkness. c - includes sleeping, loafing and preening. d - includes sexual behaviour. X - behaviour not recognised.

Species	Reference	Sample Size (Hrs)	Behaviour (%)					
			Rest	Comfort Movements	Swim/ walk	Feed	Alert	Parental Care
Greater Snow Goose	Giroux *et al* (1986)	16	16	7	12	25	40	1
Moffitt's Canada Goose	Eberhardt *et al* (1989)	186	21	11	27	41	X	X
Mallard - lake 1	Asplund (1981)	9	20	11	44	20	5	X
Mallard - lake 2	Asplund (1981)	3	0	9	64	28	0	X
Pintail	Rushforth Guinn and Batt (1985)	97	<2	9	X	52	12	23
Lesser Scaup	Afton (1983) [a]	613	25	12	18	18	23	1
Velvet Scoter	Kurilovich and Tarkhanova (1986)	Not stated	30 [b]	5	6	22	24	X
White-winged Scoter	Brown and Fredrickson (1987)	18	11	13	15	29	23	1
Goldeneye	Kurilovich and Tarkhanova (1986)	Not stated	29 [b]	6	7	22	29	X
Ruddy Duck	This study	129	21	5	35	29	5	5
Ruddy Duck - single female	Gray (1980)	3	80 [c]		13	12	X	1 [d]
Ruddy Duck - paired female	Gray (1980)	1	51 [c]		22	28	X	1 [d]
Maccoa Duck	Siegfried *et al* (1976a)	14	27	10	13	51	X	X

Siegfried *et al* (1976a) did not recognise alert behaviour whilst only Rushforth Guinn and Batt (1985) and this study recognised leading and following as distinct activities. In addition, most of the studies quoted have small sample sizes.

4.4.2 Effect of Age of Brood on Behaviour

All brood females showed significantly different levels of at least one major behaviour between the three brood ageclasses (MW U-Tests, $p<0.05$), but these differences were generally inconsistent between brood females (Table 4.6). Figures 4.2 and 4.3 summarise the change in brood female behaviour with increasing brood ageclass. Resting was lower when accompanying ageclass 1 than ageclass 2 ducklings, but the differences were not significant for any bird. Brood female 4 rested significantly less while accompanying ageclass 3 ducklings. There were no significant correlations between the level of resting behaviour and brood age (Table 4.7). Comfort movements tended to increase with increasing offspring age, but only significantly so in female 3. Feeding activity tended to decrease with increasing brood age, but only significantly so in female 3. Female 3 showed a significant positive correlation between brood age and swim whilst there were non-significant negative correlations in the other three females. There was a significant negative correlation between swimming activity and brood ageclass in female 4.

Alert behaviour in brood female 1 was significantly lower with younger ducklings and female 4 showed significantly less alert with ageclass 1 than ageclass 2 ducklings. On the contrary, female 2 spent significantly more time alert with ageclass 1 than ageclass 2 ducklings. These findings are further emphasised by significant positive correlations between alert behaviour and both brood age and ageclass in female 1 and similar significant negative correlations in female 2.

Parental care behaviour did not differ significantly between ageclasses (MW U-Tests, $p>0.05$) either when the three constituent behaviours were analysed separately or as a whole (Tables 4.6 and 4.8). However, female 4 showed a significant negative correlation between the level of parental care and brood age/ageclass (Tables 4.7 and 4.9, Fig. 4.2). The three individual parental care behaviours all showed negative correlations with brood age and ageclass except follow in female 2, but these were only significant for lead and social interaction in female 4 (Table 4.9, Fig. 4.3).

TABLE 4.6. Diurnal time budget (percent time in activity) of brood female Ruddy Duck at MSWNR - partitioning of major activities by ageclass. * - not included in KW or MW U-Tests due to small sample size. For each female, means with different letters are significantly different between ageclasses (MW U-Tests, $p<0.05$).

	No. of obs. periods	ACTIVITY											
		Rest		Comfort Movements		Swim		Feed		Alert		Parental Care	
		Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Female 1													
Ageclass 1	13	17.39	7.470	5.40	1.917	35.39	4.684	35.51	6.278	1.51 a	0.808	4.74	1.478
2	21	22.16	7.263	4.00	0.995	39.32	4.228	19.86	3.438	4.94 b	1.412	9.07	2.044
3	37	22.53	5.372	6.74	1.466	32.69	2.689	22.54	3.774	5.64 b	1.257	8.01	1.897
Female 2													
Ageclass 1	19	3.22	2.157	3.53	0.735	38.50	2.835	30.06	3.185	14.55 a	4.399	8.90	2.362
2	33	14.47	4.785	5.95	2.399	31.94	2.352	30.90	3.399	6.29 b	1.589	10.09	1.684
3 *	2	3.19	3.192	8.19	7.498	31.50	0.850	57.12	9.840	0	-	0	-
Female 3													
Ageclass 1 *	8	19.34	9.846	2.89	1.491	28.50	3.218	43.33	8.736	4.59	1.437	1.34	0.634
2	50	20.23	4.246	4.67 a	0.894	39.86	2.504	27.17 a	3.488	5.30	0.788	2.23	0.402
3	40	25.65	5.130	8.00 b	1.492	42.65	3.743	15.66 b	2.811	5.31	1.371	1.63	0.309
Female 4													
Ageclass 1	22	15.03 a	5.165	2.56	0.604	33.03	2.929	42.17 a	5.932	1.13 a	0.330	5.85	2.602
2	41	30.11 a	5.601	4.05	0.747	31.64	2.375	27.40 b	3.334	3.69 b	0.772	3.04	0.538
3	24	9.57 b	4.413	4.56	1.896	32.03	2.538	49.39 a	4.513	2.01 ab	0.604	1.91	0.563
4 *	9	55.03	14.790	5.84	2.181	12.94	3.919	24.12	11.238	0.53	0.266	0.17	0.063

TABLE 4.7. Diurnal time budget of brood female Ruddy Duck at MSWNR - Spearman's correlation coefficients between major behaviours and age of brood and time of day. *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$.

	N	Age of Brood (Days)	Ageclass	Time of Day
Rest				
Female 1	71	0.108	0.057	0.037
2	54	0.117	0.205	-0.002
3	98	0.025	0.113	-0.047
4	96	0.046	0.066	-0.241 *
Comfort Movements				
Female 1	71	0.149	0.142	0.134
2	54	-0.069	0.042	-0.085
3	98	0.235 *	0.262 **	0.070
4	96	0.078	0.068	-0.075
Swim				
Female 1	71	-0.161	-0.096	0.134
2	54	-0.265	-0.260	0.216
3	98	0.221 *	0.156	-0.127
4	96	-0.158	-0.204 *	0.105
Feed				
Female 1	71	-0.128	-0.156	0.136
2	54	0.218	0.109	-0.024
3	98	-0.263 **	-0.305 **	0.147
4	96	0.020	0.022	0.205 *
Alert				
Female 1	71	0.237 *	0.296 *	-0.086
2	54	-0.469 ***	-0.377 **	0.240
3	98	-0.040	-0.106	-0.258 *
4	96	0.023	-0.042	0.289 ***
Parental Care				
Female 1	71	-0.156	-0.053	-0.262 *
2	54	-0.034	-0.059	-0.164
3	98	-0.052	-0.084	-0.094
4	96	-0.348 ***	-0.356 ***	0.239 *

TABLE 4.8. Diurnal time budget (percent time in activity) of brood female Ruddy Duck at MSWNR - partitioning of parental care activities by ageclass. * - not included in KW or MW U-Tests due to small sample size. For each female, means with different letters are significantly different (MW U-Tests, $p<0.05$) between ageclasses.

	No. of obs. periods	ACTIVITY									
		Alert		Parental Care		Social Interaction		Lead		Follow	
		Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Female 1											
Ageclass 1	13	1.51 a	0.808	4.74	1.478	1.47	0.398	1.80	0.872	1.47	0.719
2	21	4.94 b	1.412	9.07	2.044	2.86	0.81	4.15	1.296	2.06	0.818
3	37	5.64 b	1.257	8.01	1.897	3.01	1.10	3.23	1.112	1.77	0.740
Female 2											
Ageclass 1	19	14.55 a	4.399	8.90	2.362	1.82	0.351	5.68	1.733	1.40	0.646
2	33	6.29 b	1.589	10.09	1.684	2.12	0.705	6.77	1.386	1.20	0.232
3 *	2	0	-	0	-	0	-	0	-	0	-
Female 3											
Ageclass 1 *	8	4.59	1.437	1.34	0.634	0.32	0.161	0.90	0.429	0.13	0.101
2	50	5.30	0.788	2.23	0.402	0.87	0.225	0.95	0.263	0.42	0.081
3	40	5.31	1.371	1.63	0.309	0.70	0.166	0.70	0.166	0.40	0.133
Female 4											
Ageclass 1	22	1.13 a	0.330	5.85	2.602	1.17	0.529	4.40	2.291	0.28	0.093
2	41	3.69 b	0.772	3.04	0.538	0.79	0.128	1.33	0.376	0.92	0.239
3	24	2.01 ab	0.604	1.91	0.563	0.70	0.303	0.74	0.323	0.47	0.137
4 *	9	0.53	0.266	0.17	0.063	0.17	0.063	0	-	0	-

TABLE 4.9. Diurnal time budget of brood female Ruddy Duck at MSWNR - Spearman's correlation coefficients between parental care activities and age of brood and time of day. *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$.

	N	Age of Brood	Ageclass	Time of Day
Alert				
Female 1	71	0.237 *	0.296 *	-0.086
2	54	-0.469 ***	-0.377 **	0.240
3	98	-0.040	-0.106	-0.258 *
4	96	0.023	-0.042	0.289 ***
Parental Care				
Female 1	71	-0.156	-0.053	-0.262 *
2	54	-0.034	-0.059	-0.164
3	98	-0.052	-0.084	-0.094
4	96	-0.348 **	-0.356 ***	0.239 *
Social Interaction				
Female 1	71	-0.125	-0.029	0.015
2	54	-0.161	-0.202	-0.132
3	98	-0.104	-0.123	-0.179
4	96	-0.242 *	-0.276 **	0.177
Lead				
Female 1	71	-0.157	-0.100	-0.246 *
2	54	-0.043	-0.060	-0.095
3	98	-0.058	-0.025	0.082
4	96	-0.306 **	-0.304 **	0.224 *
Follow				
Female 1	71	-0.152	-0.112	-0.326 ***
2	54	0.068	0.025	-0.236
3	98	-0.035	-0.048	-0.110
4	96	-0.148	-0.131	0.091

4.4.3 Effect of Time of Day on Behaviour

The major behaviours of brood female Ruddy Ducks at MSWNR did not differ in a consistent linear manner with time of day (Table 4.7). Brood female 4 showed a significant negative correlation between time of day and resting and a significant positive

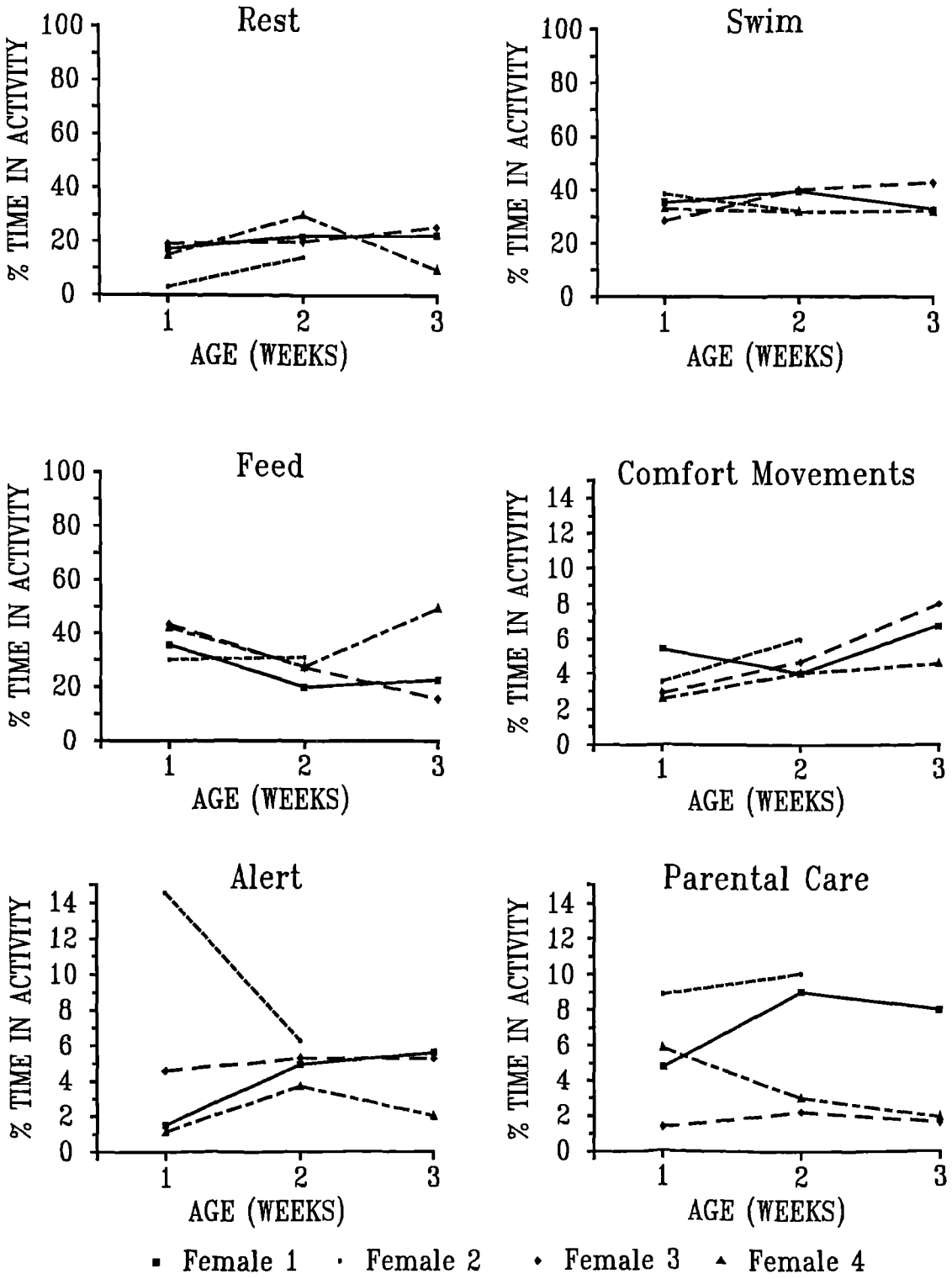

FIGURE 4.2. Change in diurnal activity of brood female Ruddy Duck at MSWNR with brood ageclass - major behaviours.

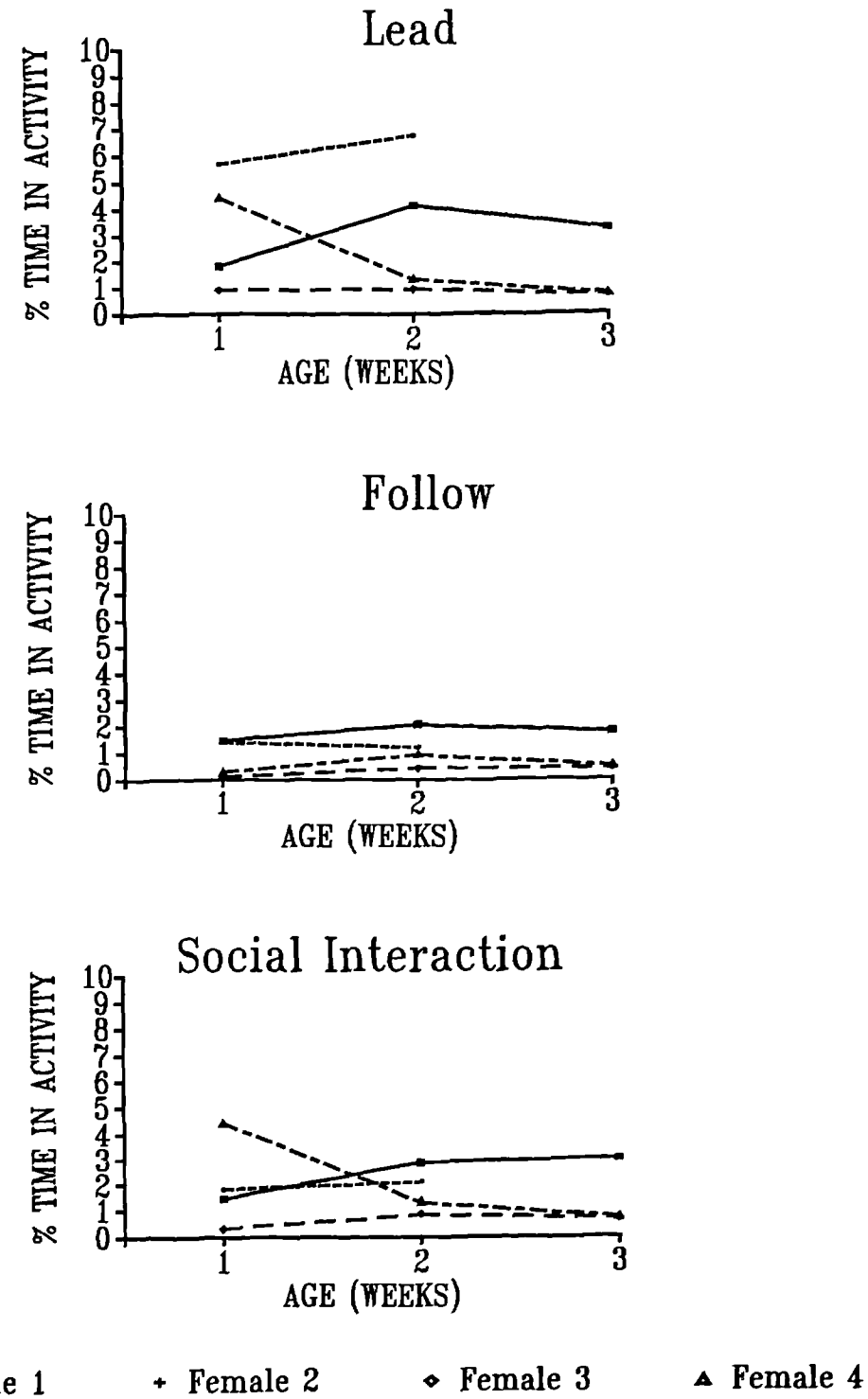

FIGURE 4.3. Change in diurnal activity of brood female Ruddy Duck at MSWNR with brood ageclass - parental care behaviours.

relationship with feed. Alert behaviour was significantly negatively correlated with time of day in female 3 and significantly positively correlated in female 4. Female 1 showed a significant negative correlation between time of day and parental care whilst female 4 showed a significant positive correlation. No other correlations between the major activities and time of day were significant.

Analysis of the individual parental care behaviours showed lead and follow to be significantly negatively correlated with time of day in female 1 and lead to be significantly positively correlated with time of day in female 4 (Table 4.9).

It is more meaningful to examine change in behaviour with time of day as a plot of mean hourly behaviour (Figures 4.4a-c). Although there was considerable variation with time of day in all females, probably due to the small sample size, it is noticeable that peaks of resting occurred in bouts during the day often following peaks in feeding activity. Feeding behaviour tended to be highest in early morning and late evening, which is especially apparent in females 3 and 4. This crepuscular feeding activity and limited nocturnal observations suggest that females and broods were also active nocturnally. Each female showed an increased period of comfort movements at some point during the day, but this was different for each bird. Usually the amount of comfort movements remained relatively constant below 10% of the hourly time budget. Swimming activity varied greatly during the day with females 1 and 3 showing notable increases towards dusk.

The level of alert and parental care varied between females with time of day and there was no common trend in either behaviour. Female 1 showed a higher level of parental care in early morning which was caused by high levels of all three individual parental care activities (Figures 4.4d and 4.4e). Female 2 also showed higher levels of lead and follow in early morning. Females 1 and 2 showed noticeably more extreme variation in lead and follow than females 3 and 4, but otherwise there was no predictable pattern in parental care behaviours between females.

4.4.4 Effect of Temperature on Behaviour

There were no significant correlations between resting or comfort movements and any of the ambient temperature variables for any of the brood females (Table 4.10).

TABLE 4.10. Diurnal time budget of brood female Ruddy Duck at MSWNR - Spearman's correlation coefficients between major behaviours and temperature variables. *, p<0.05; **, p<0.01; ***, p<0.001. a - N=58. b - N=50. c - N=44. d - N=90. e - N=88.

	N	Actual Ambient Temperature	Mean Daily Ambient Temperature	Max. Daily Ambient Temperature	Overnight Min. Ambient Temperature
Rest					
Female 1	71	0.184	0.162	0.221	0.012 [a]
2	54	0.167 [b]	0.053 [b]	-0.067	-0.171 [c]
3	98	0.178	0.055	-0.009	0.159 [d]
4	96	0.052	-0.126	0.065	0.049 [e]
Comfort Movements					
Female 1	71	0.137	0.100	0.053	0.026 [a]
2	54	-0.011 [b]	0.086 [b]	0.002	-0.149 [c]
3	98	0.183	0.059	0.078	-0.003 [d]
4	96	0.089	-0.121	-0.070	-0.146 [e]
Swim					
Female 1	71	-0.233	-0.133	0.053	-0.025 [a]
2	54	0.159 [b]	0.221 [b]	0.139	0.007 [c]
3	98	-0.340 ***	-0.284 **	-0.242 *	-0.040 [d]
4	96	-0.027	0.022	-0.052	0.256 * [e]
Feed					
Female 1	71	0.166	0.068	0.083	0.098 [a]
2	54	-0.197 [b]	-0.100 [b]	0.050	0.136 [c]
3	98	0.074	0.176	0.199	-0.172 [d]
4	96	0.044	0.225 *	0.064	-0.109 [e]
Alert					
Female 1	71	-0.339 **	-0.198	-0.184	0.100 [a]
2	54	0.197 [b]	0.265 [b]	-0.079	-0.050 [c]
3	98	-0.218 *	-0.220 *	-0.230 *	0.178 [d]
4	96	0.043	0.099	0.116	-0.103 [e]
Parental Care					
Female 1	71	-0.208	-0.154	-0.141	-0.305 * [a]
2	54	-0.294 * [b]	-0.142 [b]	-0.186	0.094 [c]
3	98	-0.111	-0.025	-0.006	0.122 [d]
4	96	-0.064	-0.070	-0.267 **	0.224 * [e]

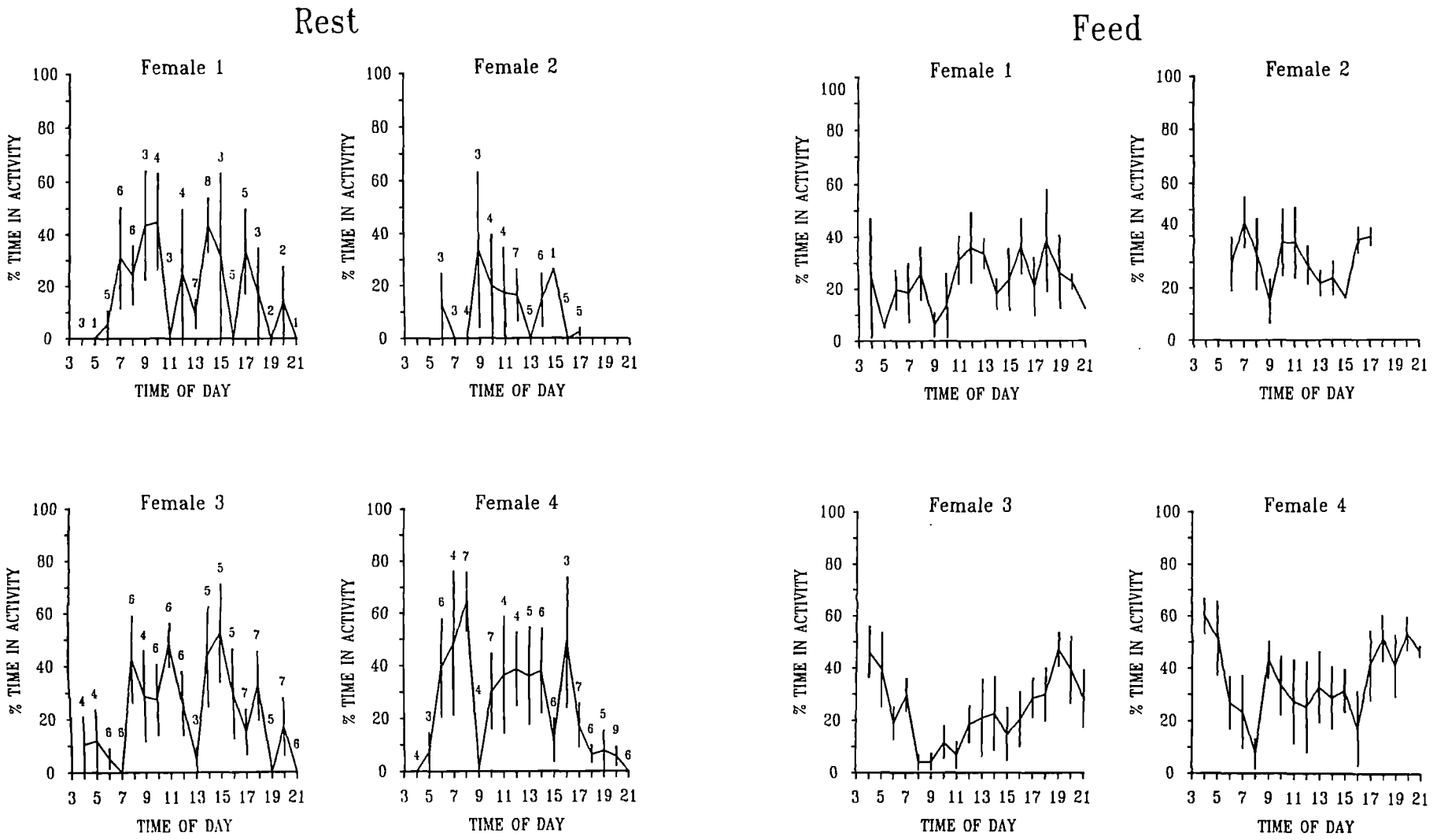

FIGURE 4.4a. Change in diurnal activity of brood female Ruddy Duck at MSWNR with time of day - rest and feed. Vertical bars represent ± 1 S.E.. Sample sizes are given above error bars.

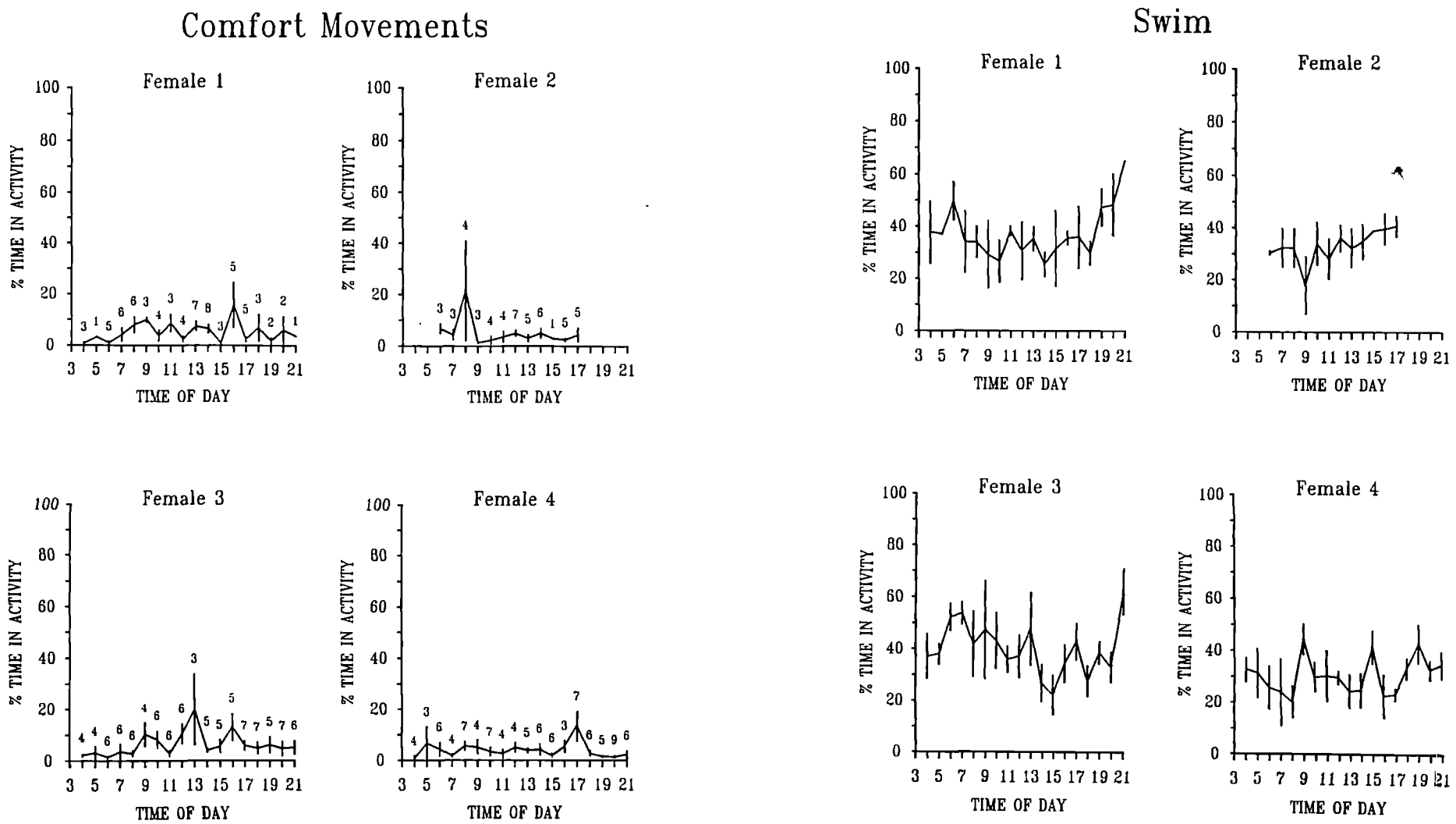

FIGURE 4.4b. Change in diurnal activity of brood female Ruddy Duck at MSWNR with time of day - comfort movements and swim. Vertical bars represent ± 1 S.E.. Sample sizes are given above error bars.

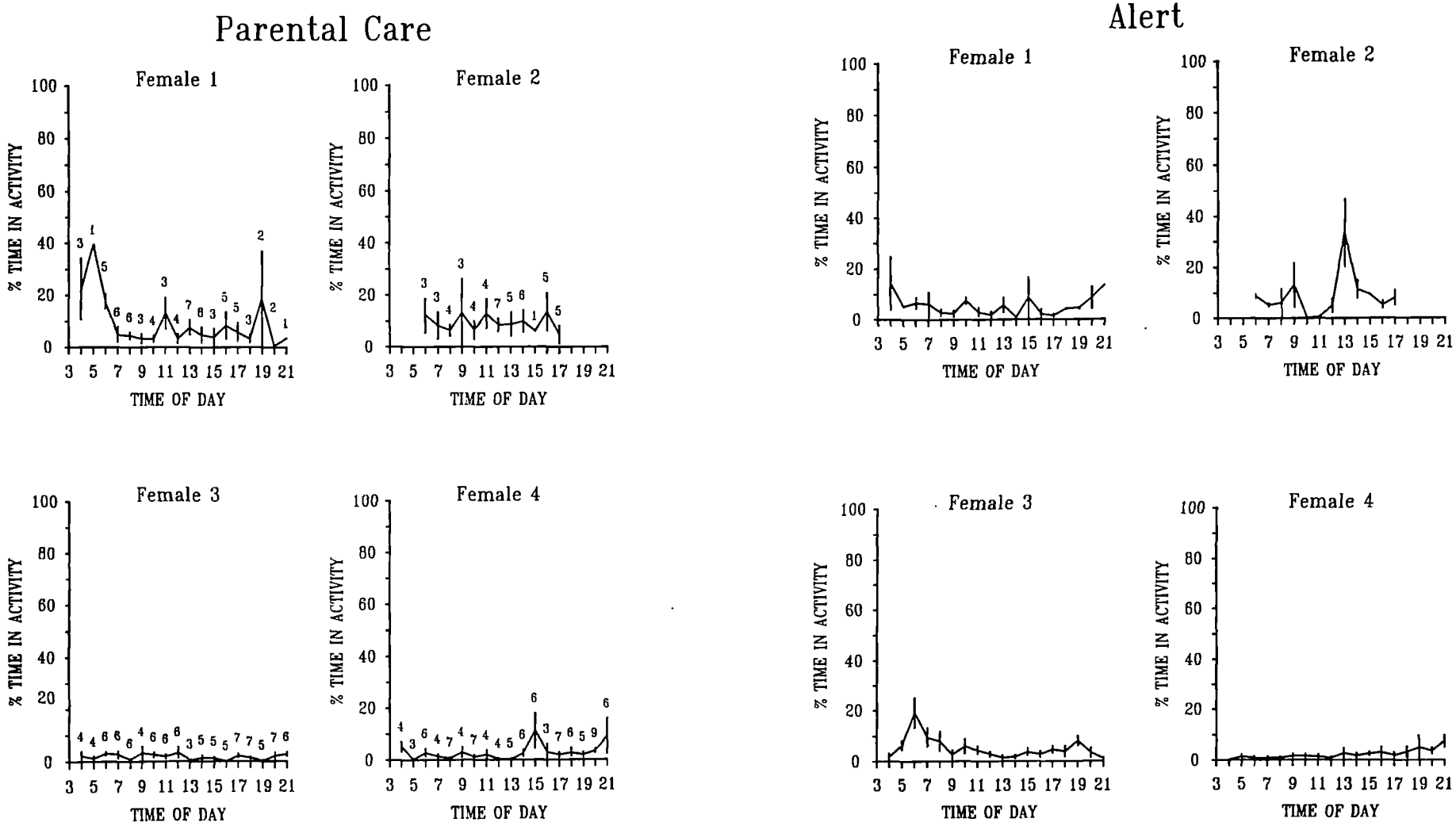

FIGURE 4.4c. Change in diurnal activity of brood female Ruddy Duck at MSWNR with time of day - parental care and alert. Vertical bars represent ± 1 S.E.. Sample sizes are given above error bars.

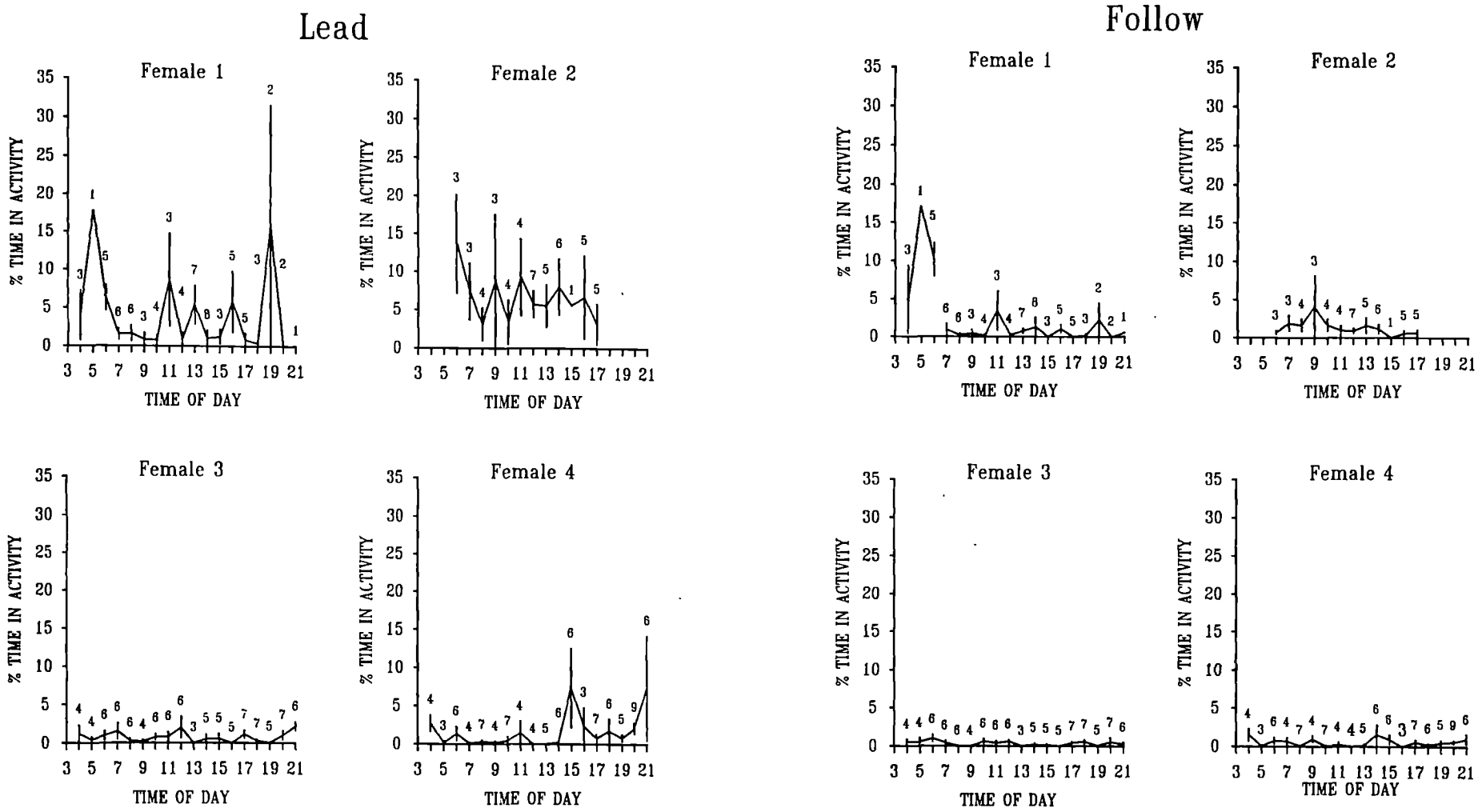

FIGURE 4.4d. Change in diurnal activity of brood female Ruddy Duck at MSWNR with time of day - lead and follow. Vertical bars represent ± 1 S.E.. Sample sizes are given above error bars.

Social Interaction

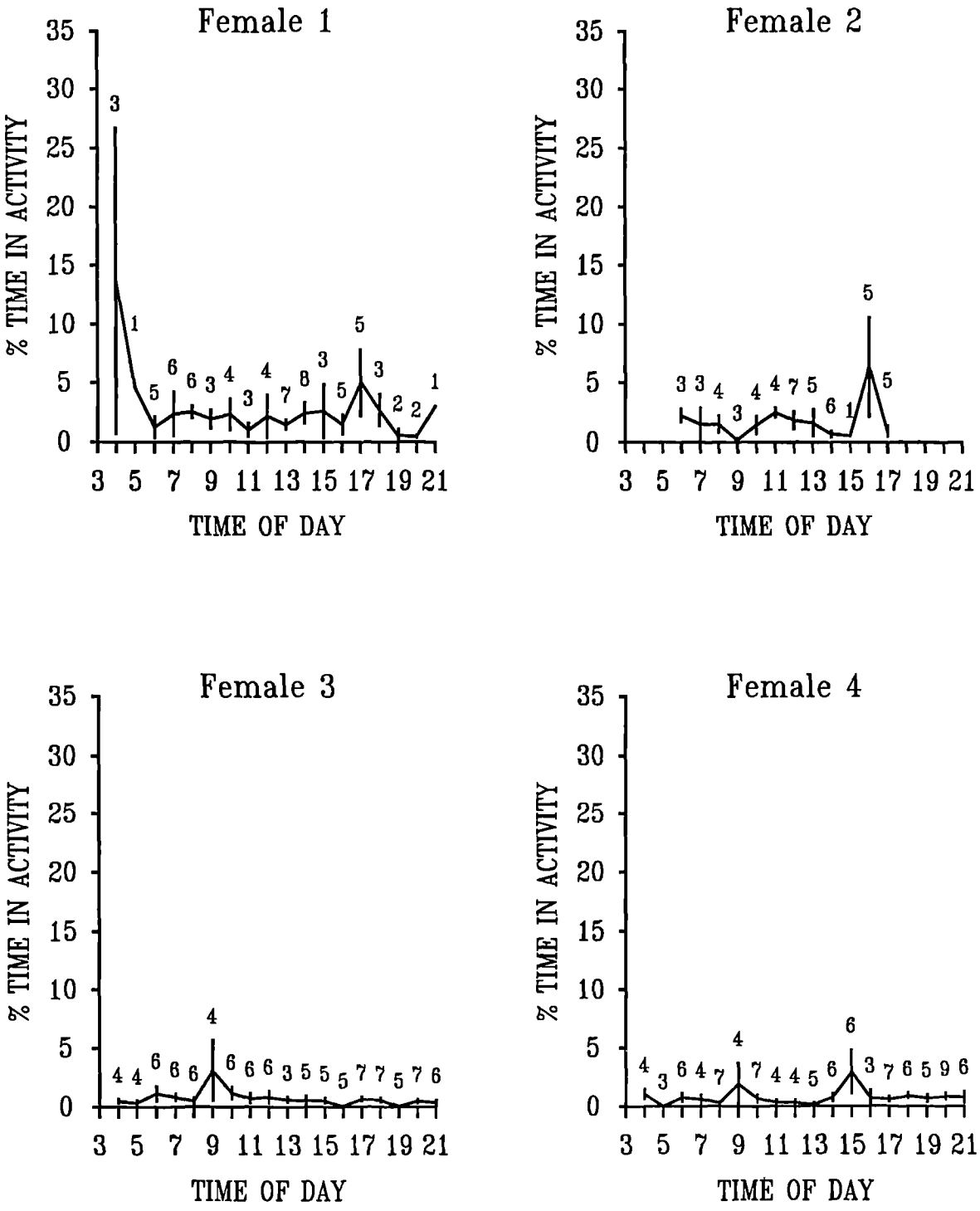

FIGURE 4.4e. Change in diurnal activity of brood female Ruddy Duck at MSWNR with time of day - social interaction. Vertical bars represent ± 1 S.E.. Sample sizes are given above error bars.

Female 3 showed significant negative correlations between swimming and actual ambient temperature, mean daily ambient temperature and maximum daily ambient temperature whilst brood female 4 showed a significant positive correlation between swimming and overnight minimum ambient temperature.

Feeding was significantly positively correlated with mean daily ambient temperature in brood female 4. Brood females 1 and 3 showed significant negative correlations between alert behaviour and actual ambient temperature whilst female 3 also showed significant negative correlations with mean and maximum daily ambient temperature. Parental care was significantly negatively correlated with actual ambient temperature in brood female 2 and with maximum daily ambient temperature in brood female 4. Female 1 showed a significant negative, and female 4 a significant positive, correlation between parental care and overnight minimum ambient temperature.

The level of social interaction was significantly negatively correlated with overnight minimum ambient temperature in female 1 (Table 4.11) whilst follow was significantly negatively correlated with actual ambient temperature in females 1, 2 and 4 and with maximum daily ambient temperature in female 4.

Females 1 and 2 spent 61.3% (43.89 of 71.65 hours) and 30.9% (9.22 of 29.86 hours) of their time out of sight, but no out-of-sight analysis was performed for females 3 and 4. Females probably spent 70-80% of their time resting while out of sight, judging from limited observations of birds in vegetation, by inference from the last behaviour observed before the birds went out of sight and by the fact that birds often moved to known resting sites within emergent vegetation. Neither female 1 or 2 showed any significant correlation between ambient temperature and the amount of time spent out of sight, however, it appeared that female 1 spent more time out of sight in higher ambient temperatures whilst the converse was true for female 2.

TABLE 4.11. Diurnal time budget of brood female Ruddy Duck at MSWNR - Spearman's correlation coefficients between parental care activities and temperature variables. *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$. a - N=58. b - N=50. c - N=44. d - N=90. e - N=88.

	N	Actual Ambient Temperature	Mean Daily Ambient Temperature	Max. Daily Ambient Temperature	Overnight Min. Ambient Temperature
Alert					
Female 1	71	-0.339 **	-0.198	-0.184	-0.100 [a]
2	54	0.197 [b]	0.265 [b]	-0.079	-0.050 [c]
3	98	-0.218 *	-0.220 *	-0.230 *	0.178 [d]
4	96	0.043	0.099	0.116	-0.103 [e]
Parental Care					
Female 1	71	-0.208	-0.154	-0.141	-0.305 * [a]
2	54	-0.294 * [b]	-0.142 [b]	-0.186	0.094 [c]
3	98	-0.111	-0.025	-0.006	0.122 [d]
4	96	-0.064	-0.070	-0.267 **	0.224 * [e]
Social Interaction					
Female 1	71	0.097	0.055	0.015	-0.320 * [a]
2	54	-0.134 [b]	-0.076 [b]	-0.066	0.076 [c]
3	98	0.010	0.002	0.040	0.150 [d]
4	96	0.013	-0.017	-0.153	0.083 [e]
Lead					
Female 1	71	-0.219	-0.197	-0.199	-0.197 [a]
2	54	-0.248 [b]	-0.059 [b]	-0.114	0.110 [c]
3	98	-0.106	-0.041	-0.066	-0.149 [d]
4	96	0.006	0.012	-0.136	0.149 [e]
Follow					
Female 1	71	-0.281 *	-0.201	-0.104	-0.223 [a]
2	54	-0.329 * [b]	-0.251 [b]	-0.244	0.076 [c]
3	98	0.011	0.103	0.121	0.106 [d]
4	96	-0.260 *	-0.195	-0.282 **	0.165 [e]

4.5 DISCUSSION

4.5.1 Diurnal Time Budget

Before considering the brood female time budgets, it is important to note that the low

number of females observed, the relatively small amount of data collected per female and the resulting small sample sizes, combined with the high variability and polymodal or skewed distribution, which is inherent in time budget data, severely limited this analysis. Hence there are some theories and explanations described without statistical justification or without comparable results being obtained for all broods.

Gray (1980) observed female Ruddy Ducks throughout the breeding season and found that during the brood-rearing period they spent the majority of daylight hours resting (including preening and loafing) and less time swimming and feeding (Table 4.5). Unfortunately, most of Gray's observations were concentrated during the laying and incubation phases of the breeding cycle and the small amount of data collected during brood-rearing (four hours) prevent further interpretation. Her results differ from the results of this study which showed swimming and feeding to be the main behaviours with less resting. Siegfried *et al* (1976a) showed that brood female Maccoa Ducks also spent most of the diurnal hours feeding with less resting, but again his results were based on a sample size of only 14 hours of observation of one female.

Swimming and feeding were the predominant diurnal activities of brood female Moffitt's Canada Geese *Branta canadensis moffitti* (Eberhardt *et al* 1989) and Mallard (Asplund 1981) whilst Lesser Scaup (Afton 1983), Velvet Scoter and Goldeneye (Kurilovich and Tarkhanova 1986) spent most time resting or alert (Table 4.5). Brood female Pintail spent most of the daylight hours feeding or in parental care activity and showed an unusually low amount of resting (Rushforth Guinn and Batt 1985). In summary, feeding or resting appears to be the predominant activity of female anatids during brood-rearing whilst alert is also prominent in the time budgets of some species, especially geese (Lazarus and Inglis 1978; Giroux *et al* 1986).

It is interesting to note the higher level of alert behaviour in Lesser Scaup, Velvet Scoter, White-winged Scoter and Goldeneye compared to Ruddy Ducks. Perhaps there were more potential predators in these studies necessitating increased vigilance, but these differences may not reflect increased vigilance of the species as a whole because alert behaviour is so liable to be influenced by external factors.

Alert behaviour showed considerable variation between the brood female Ruddy Ducks

at MSWNR for just this reason. Females appeared to assume alert postures more frequently in enclosed channels or areas without good all-round visibility, such as the narrow arm of the Wader Scrape. Similarly, Joyner (1977) found that brood female Ruddy Ducks on enclosed canals were more aggressive than brood females on larger lakes. For the above reasons, the level of alert behaviour shown by brood female Ruddy Ducks is less useful as a measure of parental care than in Pintail (Rushforth Guinn and Batt 1985) or Lesser Scaup (Afton 1983).

The higher levels of parental care behaviour in females 1 and 2 were due to greater amounts of all three individual parental care behaviours. This was partly caused by the presence of a brood of Great-crested Grebes on the Washing Well in 1988, whereas none bred there in 1989. The adult Great-crested Grebes were very aggressive and were often involved in interactions with the brood female Ruddy Ducks. The higher levels of lead shown by female 2 resulted from this female regularly leading her brood over the spit of land separating the Washing Well from the Wader Scrape. Similarly, the lower amount of lead shown by both females in 1989 was due, at least in part, to the absence of this spit through higher water levels.

The different time budgets of the four females was due, in part, to the different conditions they experienced. Biotic factors affecting their behaviour included the presence/absence and abundance of potential predators, the presence/absence and abundance of non-predatory species and their aggressiveness, the physical condition of the females and the age of the brood (see below). Date of nesting, female age and brood size have also been found to affect the behaviour of brood female waterfowl (Afton 1983; Rushforth Guinn and Batt 1985; Siriwardena and Black in prep.). Physical factors, such as the amount of emergent vegetation present, water level and physical features of the lake margins, could also affect the behaviour of the females. The restricted observation regime employed at the start of the study may also have had an effect.

4.5.2 Effect of Brood Age on Behaviour

Though there was considerable variation between the behaviour of the four brood female Ruddy Ducks it may be possible to make the following generalisations about the change in behaviour with brood age. The level of resting and swimming remained relatively

constant throughout the brood-rearing period whilst feeding tended to decline and comfort movements increase.

Other brood female waterfowl have shown similar trends in activity with increasing brood age. Brood female Moffitt's Canada Geese and Lesser Scaup both showed a significant decrease in feeding behaviour with increasing brood age and brood female Lesser Scaup showed a higher level of comfort movements with older ducklings (Afton 1983; Eberhardt *et al* 1989). The amount of resting behaviour exhibited by brood female Moffitt's Canada Geese, Lesser Scaup and Goldeneye (Kurilovich and Tarkhanova 1986) tended to increase with increasing brood age, but this was only significant for Lesser Scaup. Brood age did not have any significant effect on the self maintenance behaviours of brood female Pintail (Rushforth Guinn and Batt 1985).

It is possible that the significant increase in feeding and the associated significant decrease in resting behaviour in female 4 while accompanying ageclass 3 ducklings may be due to energy demands resulting from the onset of the pre-basic moult. Female Ruddy Ducks at Abberton Reservoir, Essex are also known to moult while still accompanying their broods (R. King pers. comm.).

In assessing the change in the level of parental care with increasing brood age, the type of analysis used in this and other studies (Afton 1983; Rushforth Guinn and Batt 1985) only provides a general overview of the actual situation due to the difficulty in defining parental care and self-maintenance behaviours. Rushforth Guinn and Batt (1985) assumed comfort movements, resting and feeding to be self-maintenance behaviours, whereas they described lead, follow, alert and social interactions as parental care. As noted by Afton (1983), there are shortcomings with this assumption and this is certainly the case when the same logic is applied to Ruddy Ducks. All behaviours shown by brood female Ruddy Ducks could be classified as parental care to some extent because of the ducklings tendency to mimic the behaviour of the brood female. Ducklings regularly preened, fed and rested in response to the initiation of these behaviours by the female.

The interpretation of changes in the level of alert behaviour as a measure of parental care is confused by the susceptibility of this behaviour to external influence. For example, much of the alert behaviour shown by female 4 was in response to the presence of Lesser

Black-backed Gulls in the study area. Therefore the levels of alert behaviour in this case may reflect gull activity rather than any trend in Ruddy Duck behaviour. Ruddy Duck females 1 and 4 showed significantly higher levels of alert behaviour while accompanying ageclass 2 than ageclass 1 ducklings whilst female 2 showed significantly less. These differences in the levels of alert activity are further indications of the influence of external factors.

All of the brood female Ruddy Ducks at MSWNR appeared to become less attentive and show less alert behaviour as the break-up of the female-brood bond approached, although this was not borne out by the statistical analysis, probably due to the factors mentioned above and the limitations of the analysis discussed at the beginning of section 4.5.1.

Alert behaviour decreased with increasing brood age in Lesser Scaup (Afton 1983), Goldeneye and Velvet Scoter (Kurilovich and Tarkhanova 1986) and Pink-footed Geese *Anser brachyrhynchus* (Lazarus and Inglis 1978) whilst Rushforth Guinn and Batt (1985) found that Pintail brood hens spent more time alert with Class II than Class I broods.

Parental care behaviours of brood female Ruddy Ducks at MSWNR tended to decline with increasing brood age, but only significantly so in female 4. A similar situation has been found for Pintail and Lesser Scaup brood hens which spent more time in parental care activities with younger ducklings (Rushforth Guinn and Batt 1985; Afton 1983). Ruddy Duck brood females tended to spend less time leading and following older ducklings whilst Pintail brood females also spent significantly less time following older ducklings and less time leading older ducklings in early season (Rushforth Guinn and Batt 1985).

The change in individual parental care behaviours with increasing brood age is discussed further in section 4.5.3.

In conclusion, the change in the behaviour of brood female waterfowl with increasing brood age appears to be fairly consistent between species. During the brood-rearing period, females tend to feed most immediately after hatching, at which time their offspring are most vulnerable. This suggests that the most important pressure at this time is to replenish endogenous reserves metabolised during incubation. Females compensate for this enforced constraint on parental care by simultaneously showing higher levels of alert

and parental care activities while not actively feeding. They also exhibit lower levels of behaviours which may be construed as "superfluous", such as resting and comfort movements. Brood female Ruddy Ducks, and brood female diving ducks in general, also modify their feeding behaviour to allow increased brood monitoring by synchronising their dives with those of their young which involves decreasing their dive length in relation to other times of the year (Joyner 1975; Ladhams 1977).

As offspring become older, acquire improved skills necessary for survival and become less dependent on the female and once females have replenished energy reserves utilized during incubation, females begin to spend more time in these "superfluous" activities and less time in parental care. This has been most effectively demonstrated in brood female Lesser Scaup, in which brood investment decreased whilst self maintenance, which included these "superfluous" activities, increased with increasing duckling age (Afton 1983).

4.5.3 Mechanism of Brood Desertion

Leading behaviour by brood females could be construed as a measure of the female's control over the position of the brood, that is, duckling dependence, while following may be a measure of the ducklings' control over the brood position, that is, duckling independence. Therefore, if increasing duckling independence was the only factor involved in the mechanism of brood desertion, one might expect to observe an increase in the level of following behaviour as broods mature. Similarly, if increasing female independence was involved then one might expect a decrease in the amount of both leading and following behaviour with increasing brood age. There is not a significant increase in following behaviour with brood age, but leading did decrease significantly in female 4. This would suggest that decreased female attentiveness is involved in the mechanism of desertion of ducklings at MSWNR. However, the fact that females showed obvious alarm as ducklings began to stray implies that duckling independence begins to increase before the brooding drive of the females decreases to any extent. In summary, the mechanism of brood desertion at MSWNR appeared to be a combination of both increasing duckling independence and decreasing female attentiveness as has been suggested for Ruddy Ducks in North America (Misterek 1974; Joyner 1975, 1977; Siegfried 1977).

Ruddy Ducks have been observed to desert their offspring as early as the first week of life (Gray 1980) or remain with them until they are completely feathered (Joyner 1969). It appears that the norm is between 3-4 weeks old (Palmer 1976; Gray 1980; this study) or 4-5 weeks old (Misterek 1974; Joyner 1977; Siegfried 1977), but the time of desertion tends to be earlier later in the breeding season (Gray 1980). Ruddy Ducks usually desert their ducklings 3-5 weeks before fledging, assuming an eight week fledging period (Misterek 1974; Joyner 1975), which is much earlier than other waterfowl, reflecting the advanced duckling independence in this species.

4.5.4 Effect of Time of Day on Behaviour

The diurnal behaviour of brood female Ruddy Ducks at MSWNR consisted of alternating bouts of feeding, preening and resting in a similar manner to that found in courting males. Siegfried (1973a) described such a cycle of behaviour when documenting the platform-building behaviour of Ruddy Ducks during the pre-nesting period. As this cycle of behaviour tended to vary in timing and duration between females and between days, there was no predictable pattern of behaviour during the mid-morning to late afternoon period. However, during early morning and evening female Ruddy Ducks and their broods became more active and tended to show increased feeding and swimming activity and an associated decrease in resting. This crepuscular peak in feeding is probably connected to the nocturnal feeding habits of Ruddy Ducks (see Chapter Two). Joyner (1977) also noted broods of Ruddy Ducks feeding most in early morning and from late evening until they could no longer be observed. Pre-laying and laying female Ruddy Ducks are also thought to feed at night (Tome 1991).

4.5.5 Effect of Temperature on Behaviour

Throughout the study brood female Ruddy Ducks appeared to be less active during periods of high ambient temperature, although only female 3 showed a significant negative correlation between swimming activity and ambient temperature. All four birds showed positive correlations between resting behaviour and ambient temperature, but none were significant. These results and the fact that all other significant correlations between actual ambient temperature and activity were negative suggests reduced activity with increasing ambient temperature, but the small sample size and high variance of the data limited the

analysis. The situation is further confused by the Ruddy Duck's habit of spending a significant amount of time out of sight in lakeside vegetation. Both females analysed for out-of-sight behaviour spent a high proportion of their diurnal time budget out of sight, especially so in female 1 which experienced consistently higher temperatures than female 2. Mallard have also been found to spend more time out of sight at higher ambient temperatures (Ringelman and Flake 1980). Follow showed a negative correlation with actual ambient temperature in three of the brood females and this is probably a function of the females inactiveness at higher temperatures.

While out of sight, females appeared to spend most of their time resting as has been found for Lesser Scaup (Afton 1983).

It is possible that low overnight ambient temperatures could increase the amount of diurnal feeding necessary by causing a reduced availability of invertebrate prey during the preferred nocturnal feeding period as the main prey of Ruddy Ducks, chironomids, are known to show a negative correlation between temperature and adult emergence (Wrubleski and Ross 1989). However, there was no relationship between the amount of diurnal feeding and overnight minimum ambient temperature. Other correlations between activity and overnight minimum ambient temperature were inconsistent between females and more likely to be spurious effects of the small sample size.

CHAPTER FIVE.

DIURNAL SOCIAL INTERACTION IN RUDDY DUCKS.

5.1 INTRODUCTION

Ruddy Ducks, especially brood females, are known to be aggressive in captivity (N.S. Jarrett pers. comm.) and in the wild in North America (Joyner 1975, 1977). Gray (1980) studied the agonistic behaviour of male Ruddy Ducks throughout the breeding season in California and Joyner (1975, 1977) provided information on social interactions of brood female Ruddy Ducks in Utah. Both authors found high levels of intra- and interspecific interaction. Should an available niche in the British wetland ecosystem not exist for the Ruddy Duck, then competition might be expected with native waterbirds, especially during the breeding season as they prefer similar breeding habitat to grebes, ducks, Coot and Moorhen.

This chapter provides a description of the number, duration, and intensity of intra- and interspecific interactions involving Ruddy Ducks in Great Britain during the non-breeding, courtship and brood-rearing periods. The change in the three social interaction parameters is assessed with time of day and date/pairing status in courting male Ruddy Ducks and with time of day and brood age in brood females.

The present and potential effects of interspecific interaction on native species of waterbird are discussed.

5.2 STUDY AREAS

Details of social interactions were collected concurrently with time budget data at CVL (see section 2.2) and MSWNR (see section 3.2).

5.3 METHODS

5.3.1 Social Interaction

Social interactions were monitored during the diurnal winter, spring and summer time budgets of 1988 and 1989 (Chapters Two, Three and Four). As social interaction data were collected concurrently with time budget data, the methods of observation were

similar.

For each interaction the following details were recorded:-

1. The species involved in the interaction.

   During the male courtship display study, there were five classes of Ruddy Duck recognised in intraspecific interactions depending on sex, plumage and pairing status in females:-

   i) Male in alternate plumage. Most of these birds were probably adult males.
   ii) Male in basic plumage. Most of these birds were probably first year birds which had not acquired first alternate plumage.
   iii) Female paired to the male under observation.
   iv) Other female.
   v) A "no details" category for which intraspecific social interaction had been registered on the event recorder, but no details of the encounter recorded.

   During the brood female study, seven classes of Ruddy Ducks were recognised in intraspecific interactions depending on age, sex, and relationship with the female under observation:-

   i) Attending male. Males accompanying females with broods. This term does not imply that the birds were paired or that the male was related to the offspring. Indeed, females may be attended by different males during brood-rearing (Gray 1980).
   ii) Other male.
   iii) Male - relationship to female undetermined.
   iv) Female.
   v) Duckling.
   vi) Multiple interactions involving more than one class of Ruddy Duck.
   vii) A "no details" category.

   A multiple interaction was also recorded if more than one species was involved in an interaction. On a small number of occasions it was not possible to identify the other species involved in the interaction.

2. The initiator of the interaction.

Four classes of initiation were recognised:-

i) Initiated by study bird.

ii) Initiated by other bird.

iii) Initiator unknown.

iv) Avoidance.

3. The victor of the interaction.

i) Won by focal individual.

ii) Won by other bird.

iii) Victor unknown.

iv) Avoidance (hence no victor).

4. The intensity of the interaction.

Intensity was scored on a five point scale.

1. **"Swam at"** bird. The lowest grade of intensity in which the Ruddy Duck simply swims at another bird without apparent aggression. Other birds are, however, forced to retreat short distances in avoidance.
2. **Hunched Threat** (Gray 1980). Ruddy Ducks assume a hunched posture with the head low to the surface of the water and extended slightly forward. The body feathers are puffed out and the scapulars and ear tufts raised resulting in an apparent increase in body size.
3. **Open-billed Threat**. The Hunched Threat posture is assumed and the bill opened towards the rival. This posture is often accompanied by a hissing sound.
4. **Hunched Rush** (Gray 1980). Birds assume the Open-billed Threat posture then rush across the surface of the water towards the opponent. In contrast to the courtship display Display Flight, the wings remain closed during the Hunched Rush and propulsion is provided by the feet alone.
5. **Physical contact**. This category includes all interactions in which there is either actual physical contact between birds or an attempt to make physical contact.

    i) **Attempt to Peck**. Focal individuals peck at other birds, but do not make any physical contact.

ii) **Peck.** The first grade of intensity in which actual physical contact occurs. Focal individuals physically peck their opponent.

iii) **Fight.** Fighting only resulted when opponents did not retreat in response to lower levels of aggression.

The duration of each social interaction was extracted from the time budget data for this analysis.

5.3.2 Data Analysis

The analysis of winter social interactions was limited to a descriptive nature by the small number of interactions recorded. Likewise, all three sex/plumage classes of Ruddy Duck (alternate male, basic male and female/juvenile) were treated together.

After initial consideration of the data, the change in the number, duration and intensity of social interaction was investigated with time of day and date in courting males and with time of day and brood age in brood females. Avoidance interactions, multiple interactions and records with missing values were excluded from the analysis.

For the analysis, time of day was divided into four three-hour periods for courting males and six for brood females:-

Courting Males

1. Early morning - 0600-0859h.
2. Late morning - 0900-1159h .
3. Afternoon - 1200-1459h.
4. Evening - 1500-1859h.

Brood Females

1. Early morning - 0400-0659h.
2. Late morning - 0700-0959h.
3. Noon - 1000-1259h.
4. Early afternoon - 1300-1559h.
5. Late afternoon - 1600-1859h.
6. Evening - 1900-2159h.

Expected values of the number of social interactions per time, date or brood age category were calculated by proportioning the total number of observations in relation to the length of observation per category. This assumes that the number of interactions was directly related to the length of observation. The number of other birds present was not evaluated

and hence expected values of social interaction did include consideration of the probability of encounter. Expected values were compared to 95%, 99% and 99.9% confidence intervals calculated from the observed distributions. Rates of interaction in the time of day, date and brood age analyses were calculated by summing interactions by category and dividing by the total time of observation per category.

Throughout the duration analyses parametric statistics were used whenever possible, that is, whenever the assumptions of independence, normality and homogeneity of group variances were fulfilled. Non-parametric statistics were employed when the assumptions were not met. Parametric tests used were one-way and two-way ANOVA, Duncan's multiple range test and Pearson's correlation. Non-parametric tests were Kruskal-Wallis analysis of variance, Mann-Whitney U-test and Spearman's correlation. Although log-transformed duration values were used in many parametric tests, mean durations from the original data are quoted in the text and used in figures. It may have been more acceptable statistically to quote back-transformed mean log values, but this would have no direct biological significance.

Intensity analysis was performed for only those interactions initiated by focal birds because relevant details for other birds involved, such as pairing status, could not be recorded given that social interaction data and time budget data were being collected simultaneously. Interactions involving a number of different intensities were scored as the highest intensity value. As well as avoidance interactions, passive interactions, such as those initiated by birds surfacing under others, were not included in the intensity analysis. Because the intensity values were classified in an artificial manner and non-normally distributed, non-parametric statistics were used to test for differences in interaction intensity.

5.3.3 Appeal for Interspecific Social Interaction Information

A general appeal for information on interspecific social interactions of Ruddy Ducks was circulated to bird clubs in all areas of Great Britain where Ruddy Ducks have occurred. A similar appeal also appeared in two national birdwatching magazines, **Birding World** and **BTO News**. The appeal requested the following information:-

1. The other species involved in the interaction.
2. The initiator of the interaction.
3. The victor of the interaction.
4. The short-term results of the interaction, for example, desertion of a nest or displacement of the loser from a site.
5. The long-term effect of the interaction, for example, a decline in numbers of a species or a decline in breeding success.

Responses from the appeal are not given in detail in the results section, but referred to in the discussion at the end of this chapter.

5.4 RESULTS

5.4.1 Winter Social Interaction

Social interactions observed during the winter time budget are summarised in Table 5.1. During the winter, there were only 75 interactions in 124.6 hours of observation. The majority (61.3%) were intraspecific. Interactions with males constituted 74.3% (26/35) of all intraspecific encounters for which details were recorded compared to 25.7% (9/35) with females.

Six species were involved in 23 interspecific interactions with Ruddy Ducks, most of which (87.0%) were initiated by the other species. Most interspecific interactions involved Black-headed and Common Gulls which arrived in late afternoon to roost on the lake. As the gulls flew over they often stooped to dive-bomb Ruddy Ducks and other waterbirds. Only one interspecific interaction was initiated by a Ruddy Duck. This involved a female/juvenile bird which showed an Open-billed Threat towards a Black-headed Gull. Wintering Ruddy Ducks showed avoidance reactions on two occasions.

5.4.2 Courting Male Social Interaction

5.4.2.1 Number of Interactions

5.4.2.1.1 Initial Considerations

Social interactions observed during the courting male time budget are summarised in Table 5.2. All males selected for observation were in alternate plumage. During the

TABLE 5.1. Social interactions recorded during the winter diurnal time budget at CVL. Number of hours of observation = 124.6. a - values calculated as a percentage of total interactions (intraspecific + interspecific).

Species	Initiated by Study Bird		Initiated by Other Bird		Avoidance		Total	
	No.	% [a]	No.	%	No.	%	No.	%
Intraspecific								
Male	15	20.0	11	14.7	0	0	26	34.7
Female	4	5.3	5	6.7	0	0	9	12.0
No details	10	13.3	1	1.3	0	0	11	14.7
TOTAL	29	38.7	17	22.7	0	0	46	61.3
Interspecific								
Teal	0	0	0	0	1	1.3	1	1.3
Pochard	0	0	1	1.3	0	0	1	1.3
Coot	0	0	2	2.7	0	0	2	2.7
Black-headed Gull	1	1.3	11	14.7	0	0	12	14.7
Common Gull	0	0	5	6.7	1	1.3	6	8.0
Lesser Black-backed Gull	0	0	1	1.3	0	0	1	1.3
TOTAL	1	1.3	20	26.7	2	2.7	23	30.7
Species unknown	0	0	6	8.0	0	0	6	8.0
GRAND TOTAL	30	40.0	43	57.3	2	2.7	75	100.0

study there were 255 interactions in 111.3 hours of observation. As in the winter, the majority (92.9%) were intraspecific with 81.0% (188/232) of the intraspecific encounters for which details were recorded involving male-male interactions. Males initiated most of the interactions involving females, although no paired males showed any hostility towards their mates. Paired females initiated five interactions towards their mates.

Seven species were involved in 17 interspecific interactions with courting male Ruddy Ducks, only three of which were initiated by the other species. Males initiated interactions against Great-crested Grebe, Mallard, Pochard, Tufted Duck and Goldeneye. Only Great-crested Grebe (2 occasions) and Goldeneye (1 occasion) initiated and won interactions against male Ruddy Ducks. Male Ruddy Ducks showed avoidance reactions on three occasions.

TABLE 5.2. Social interactions recorded during the courting male time budget at MSWNR. Number of hours of observation = 111.3. a - values calculated as a percentage of total interactions (intraspecific + interspecific).

Species	Initiated by Study Bird		Initiated by Other Bird		Avoidance		Total	
	No.	% [a]	No.	%	No.	%	No.	%
Intraspecific								
Male - Alternate plumage	115	45.1	46	18.0	0	0	161	63.1
Male - Basic plumage	22	8.6	5	2.0	0	0	27	10.6
Female of pair	0	0	5	2.0	0	0	5	2.0
Other female	36	14.1	3	1.2	0	0	39	15.3
No details	5	2.0	0	0	0	0	5	2.0
TOTAL	178	69.8	59	23.1	0	0	237	92.9
Interspecific								
Great-crested Grebe	1	0.4	2	0.8	0	0	3	1.2
Greylag Goose	0	0	0	0	2	0.8	2	0.8
Mallard	1	0.4	0	0	0	0	1	0.4
Pochard	3	1.2	0	0	0	0	3	1.2
Tufted Duck	4	1.6	0	0	0	0	4	1.6
Goldeneye	2	0.8	1	0.4	0	0	3	1.2
Black-headed Gull	0	0	0	0	1	0.4	1	0.4
TOTAL	11	4.3	3	1.2	3	1.2	17	6.7
Species unknown	1	0.4	0	0	0	0	1	0.4
GRAND TOTAL	190	74.5	3	1.2	3	1.2	255	100.0

A total of 223 interactions (211 intraspecific and 12 interspecific) had no missing values and were included in further analysis. Alternate males won 98.5% (133/135) of intraspecific interactions initiated against other alternate males, 100% (20/20) of interactions initiated against basic males and 97.1% (33/34) of those initiated against "other females". Although the numbers of interactions initiated against focal alternate males by the other classes of Ruddy Duck were much smaller, all were won by the initiator (basic males 5/5, other females 3/3 and paired females 5/5).

In the period following pair formation, paired males initiated a significantly higher

proportion (82/95 versus 24/47; χ^2=18.83, d.f.=1, p<0.001) and won a significantly higher proportion (79/92 versus 20/43; χ^2=21.24, d.f.=1, p<0.001) of interactions than single males.

5.4.2.1.2 Effect of Time of Day

The distribution of the number of social interactions involving courting male Ruddy Ducks differed significantly from the expected distribution calculated from the total time of observation per time period. Males showed significantly fewer interactions than expected in the afternoon period regardless of pairing status (Table 5.3). Paired males showed significantly more interactions than expected in the late morning period whilst single males showed significantly more in the evening. These results are reflected in the mean rate of social interaction per time period (Fig. 5.1).

TABLE 5.3. Changes in the number of social interactions of paired and single courting male Ruddy Duck at MSWNR with time of day.

Time of Observation	Number of Interactions	Observed %	Expected %	Difference	Significance
Paired Males					
Early Morning (0600 - 0859)	29	30.53	25.34	MORE	NS
Late Morning (0900 - 1159)	29	30.53	18.38	MORE	$p < 0.05$
Afternoon (1200 - 1459)	11	11.58	29.30	LESS	$p < 0.001$
Evening (1500 - 1859)	26	27.37	27.00	MORE	NS
Single Males					
Early Morning (0600 - 0859)	40	31.25	33.98	LESS	NS
Late Morning (0900 - 1159)	19	14.84	17.59	LESS	NS
Afternoon (1200 - 1459)	21	16.41	28.05	LESS	$p < 0.01$
Evening (1500 - 1859)	48	37.50	20.39	MORE	$p < 0.001$

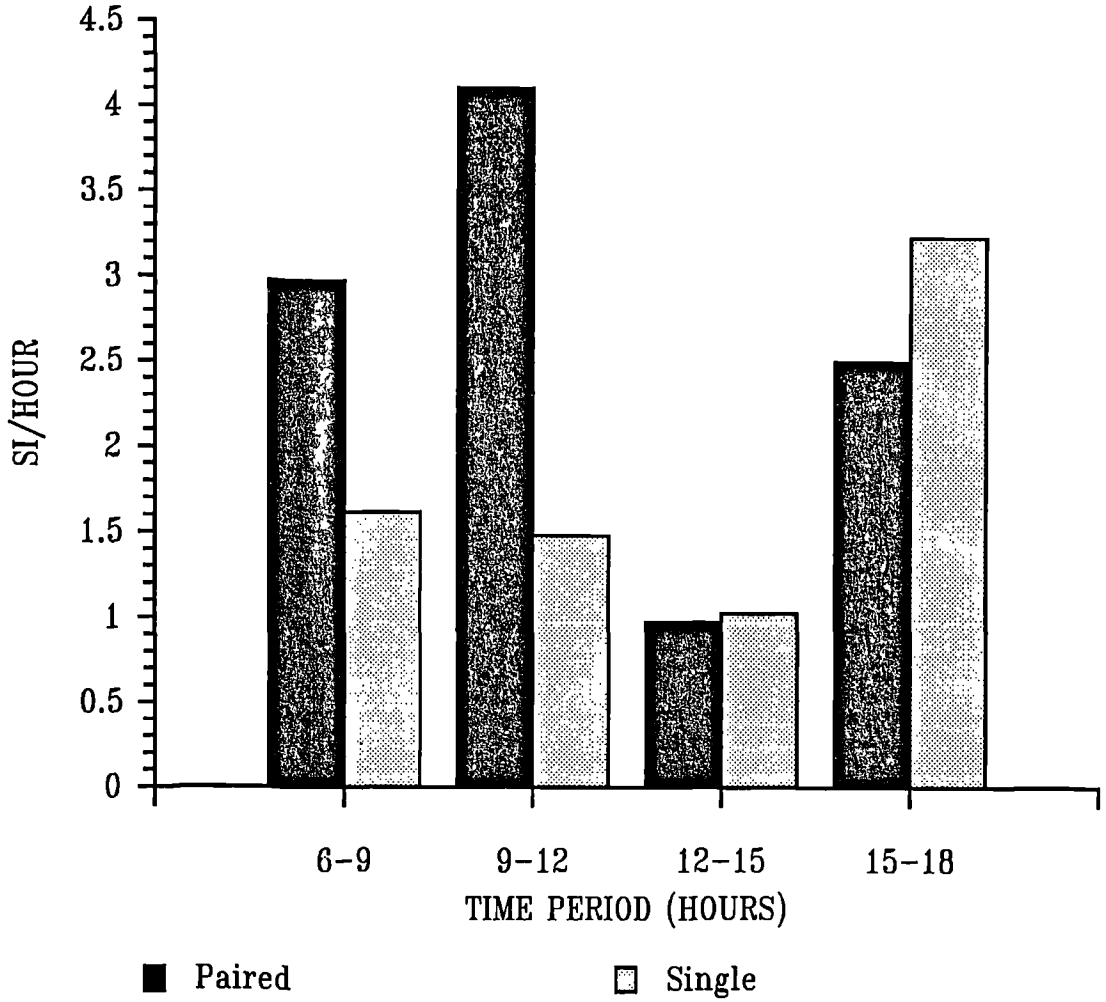

FIGURE 5.1. Change in the rate of social interaction in paired and single male Ruddy Duck during the courtship period at MSWNR with time of day.

5.4.2.1.3 Effect of Date

The distribution of the number of social interactions involving both paired and single males differed significantly from the expected distribution calculated from the total time of observation per week. Paired males were involved in significantly more interactions than expected in week 3, the first week in which paired males were observed, and significantly fewer in week 4 (Table 5.4). Single males were involved in significantly more interactions than expected in week 2 and significantly fewer in week 5. These results are illustrated in the mean rate of social interaction per week (Fig. 5.2). Paired males showed an initially high rate of interaction in week 3, a decrease in week 4 and an increase in week 5. The rate of social interaction in single birds showed two peaks in weeks 2 and 4.

TABLE 5.4. Changes in the number of social interactions of paired and single courting male Ruddy Duck at MSWNR with date.

Week of Observation	Number of Interactions	Observed %	Expected %	Difference	Significance
Paired Males					
1	0	-	-	-	-
2	0	-	-	-	-
3	35	36.84	23.66	MORE	$p < 0.05$
4	15	15.79	33.08	LESS	$p < 0.001$
5	45	47.37	43.26	MORE	NS
Single Males					
1	22	17.19	25.11	LESS	NS
2	47	36.72	24.68	MORE	$p < 0.05$
3	29	22.66	25.00	LESS	NS
4	29	22.66	17.92	MORE	NS
5	1	0.78	7.30	LESS	$p < 0.01$

5.4.2.2 Duration of Interactions

5.4.2.2.1 Initial considerations

Log-transformations were applied to duration values to obtain normality (Lilliefors Test,

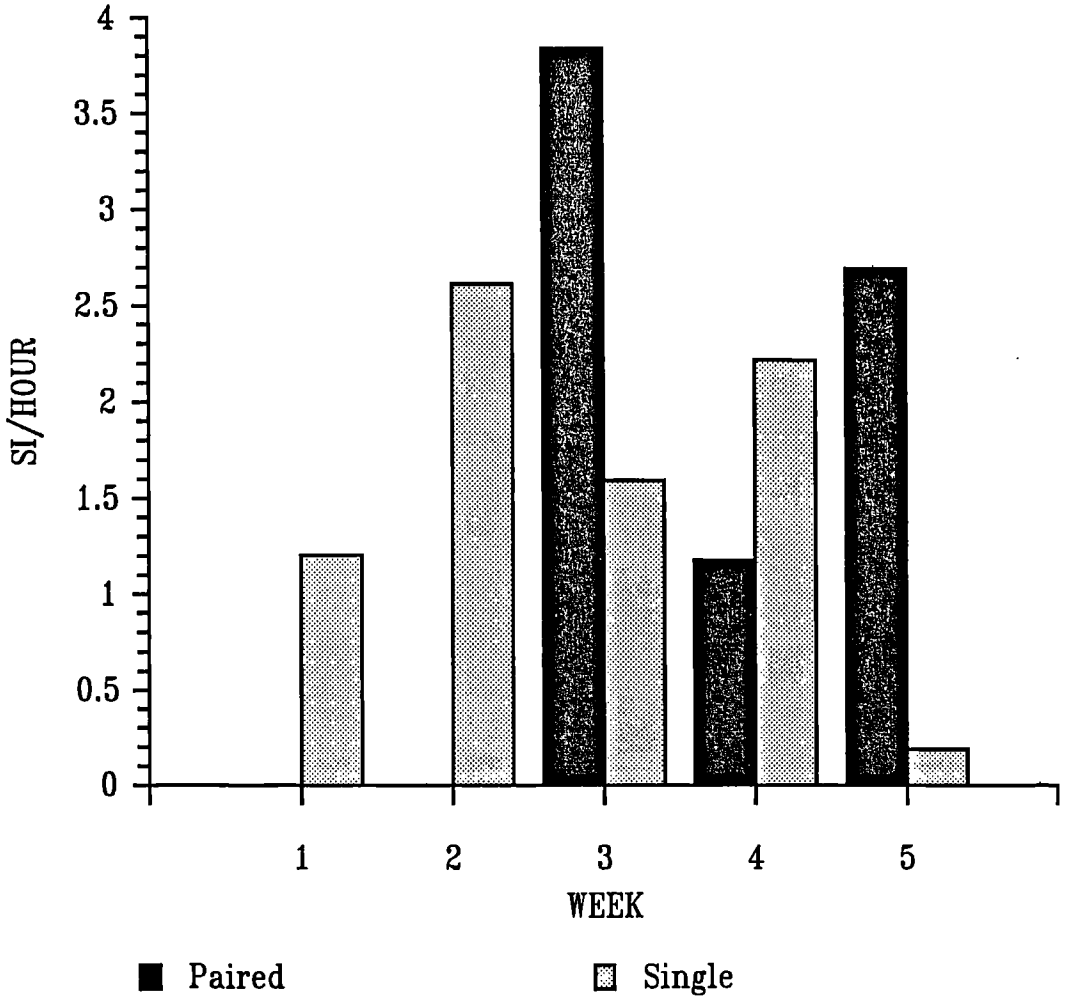

FIGURE 5.2. Change in the rate of social interaction in paired and single male Ruddy Duck during the courtship period at MSWNR with date.

$p>0.05$). Intraspecific interactions were slightly, but not significantly, longer than interspecific interactions (3.94 ± 0.247 versus 3.37 ± 0.760 seconds), therefore both classes of encounter were amalgamated for analysis.

Interactions were of similar duration regardless of the initiator or the victor (T-tests, $p>0.05$). The presence/absence of females also had no significant effect on interaction duration (T-test, $p=0.368$). Other males were absent on only two occasions so no male presence/absence analysis was performed.

Paired males were involved in significantly longer interactions than single males (4.22 ± 0.310 seconds ($n=95$) versus 3.71 ± 0.371 seconds ($n=116$); T-Test, $p<0.05$). Similarly, interactions initiated by paired focal males were significantly longer than those initiated by single focal males.

5.4.2.2.2 Effect of Time of Day

Time of day had little effect on interaction duration (Fig. 5.3). Interactions involving paired males were significantly longer in the evening than in the morning and evening paired male interactions were significantly longer than single male interactions in all time periods (T-tests, $p>0.05$).

5.4.2.2.3 Effect of Date

Interaction duration for paired males increased as the study period progressed (Fig. 5.4), significantly so between weeks 3 and 5. Similarly, paired males showed a significant positive correlation between interaction duration and week of study period ($r_p=0.358$, $N=95$, $p<0.001$). Single males showed a non-significant increase in interaction duration during the first three weeks of the study then a significant decline in week 4. Paired males were involved in significantly longer interactions than single males in week 4.

5.4.2.3 Intensity of Interactions

5.4.2.3.1 Initial Considerations

A total of 162 interactions (93.8% intraspecific and 6.2% interspecific) were initiated by study males and included in the intensity analysis. Intra- and interspecific interactions did not differ significantly in intensity and were therefore treated together in the analyses.

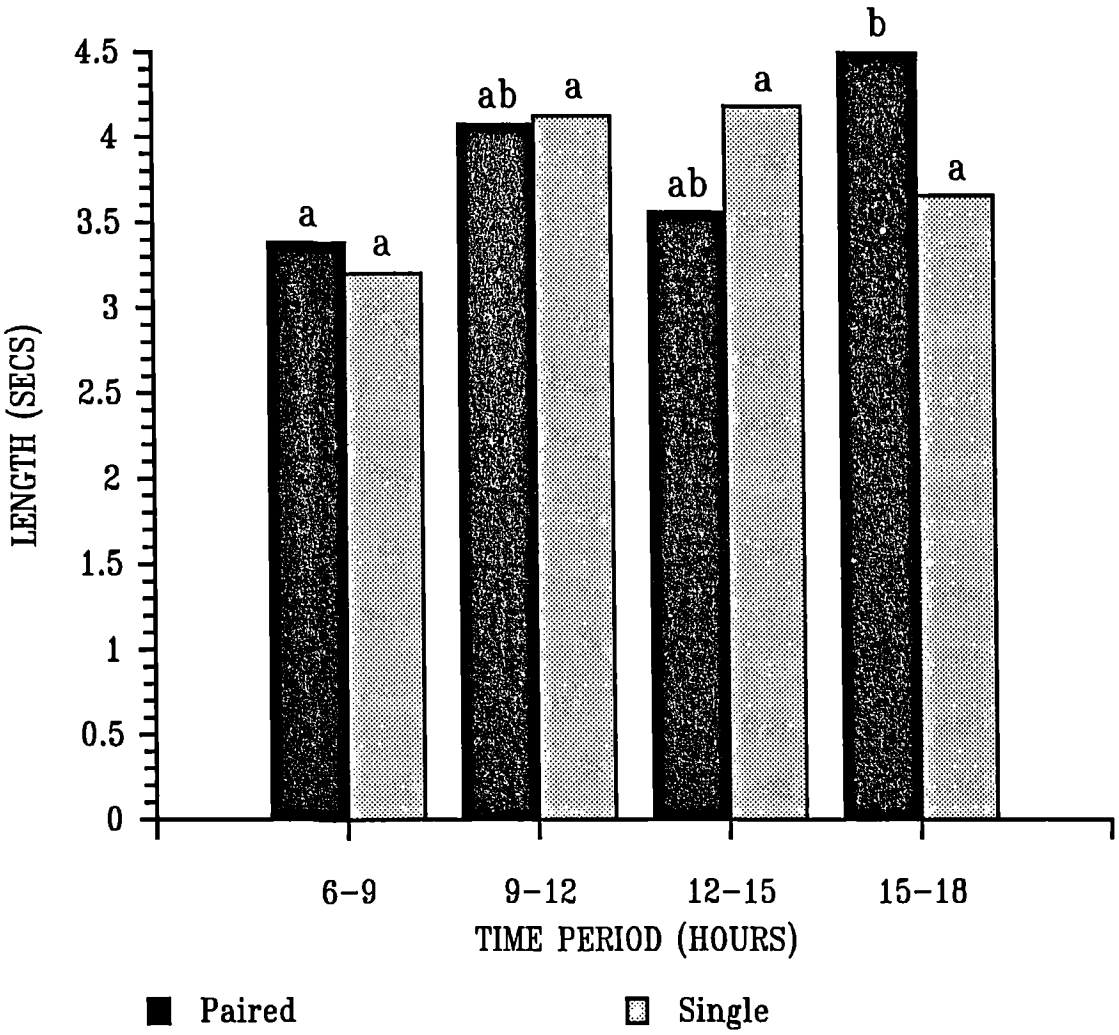

FIGURE 5.3. Change in the duration of social interactions in paired and single male Ruddy Duck during the courtship period at MSWNR with time of day. Column means with different letters are significantly different (MW U-Tests, $p<0.05$).

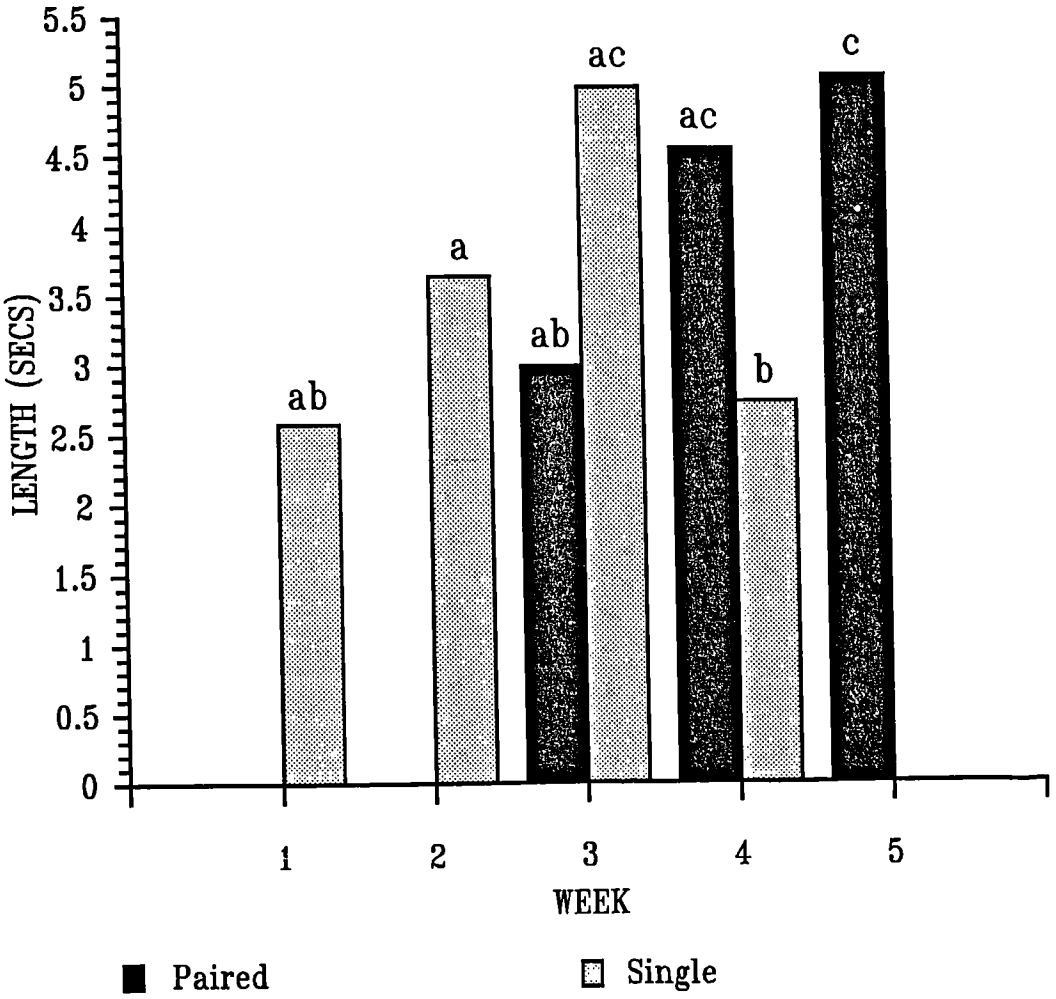

FIGURE 5.4. Change in the duration of social interactions in paired and single male Ruddy Duck during the courtship period at MSWNR with date. Column means with different letters are significantly different (MW U-Tests, $p<0.05$).

Table 5.5 provides a summary of the intensity of interactions for paired and single males. The majority of interactions were Hunched Rushes (86.6% in paired and 71.3 % in single males). Fighting was only noted in single males: three times with other alternate male Ruddy Ducks, once with a Goldeneye and twice with Pochard. Interaction intensity did not differ between paired and single males (MW U-Test, p=0.977) with both showing a mean interaction intensity of 3.7.

TABLE 5.5. Intensity of interactions of paired and single courting male Ruddy Duck at MSWNR.

Intensity	No. of Interactions (%)		
	Paired Males	**Single Males**	**All Males**
1 - Swam at	3 (3.7)	5 (6.3)	8 (4.9)
2 - Hunched Threat	8 (9.8)	2 (2.5)	10 (6.2)
3 - Open-billed Threat	0	10 (12.5)	10 (6.2)
4 - Hunched Rush	71 (86.6)	57 (71.3)	128 (79.0)
5 - Physical contact	0	6 (7.5)	6 (3.7)
TOTAL	82	80	162

Study males won 96.9% of interactions which they initiated, males were present in 99.4% and females in 95.7% of interactions, therefore no intensity analysis was performed for victor of interaction or male and female presence/absence.

5.4.2.3.2 Effect of Time of Day

Paired and single courting male Ruddy Ducks showed no significant differences in interaction intensity between the four time periods (KW Test, p=0.195). This is illustrated in Figure 5.5.

5.4.2.3.3 Effect of Date

The intensity of interactions initiated by single males was significantly less in week 3 than in weeks 2 and 4 whilst paired males showed a significant increase in interaction intensity between weeks 3 and 4 (Fig. 5.6). In weeks 3 and 4, paired males initiated interactions of higher intensity than single males, but the difference was not significant.

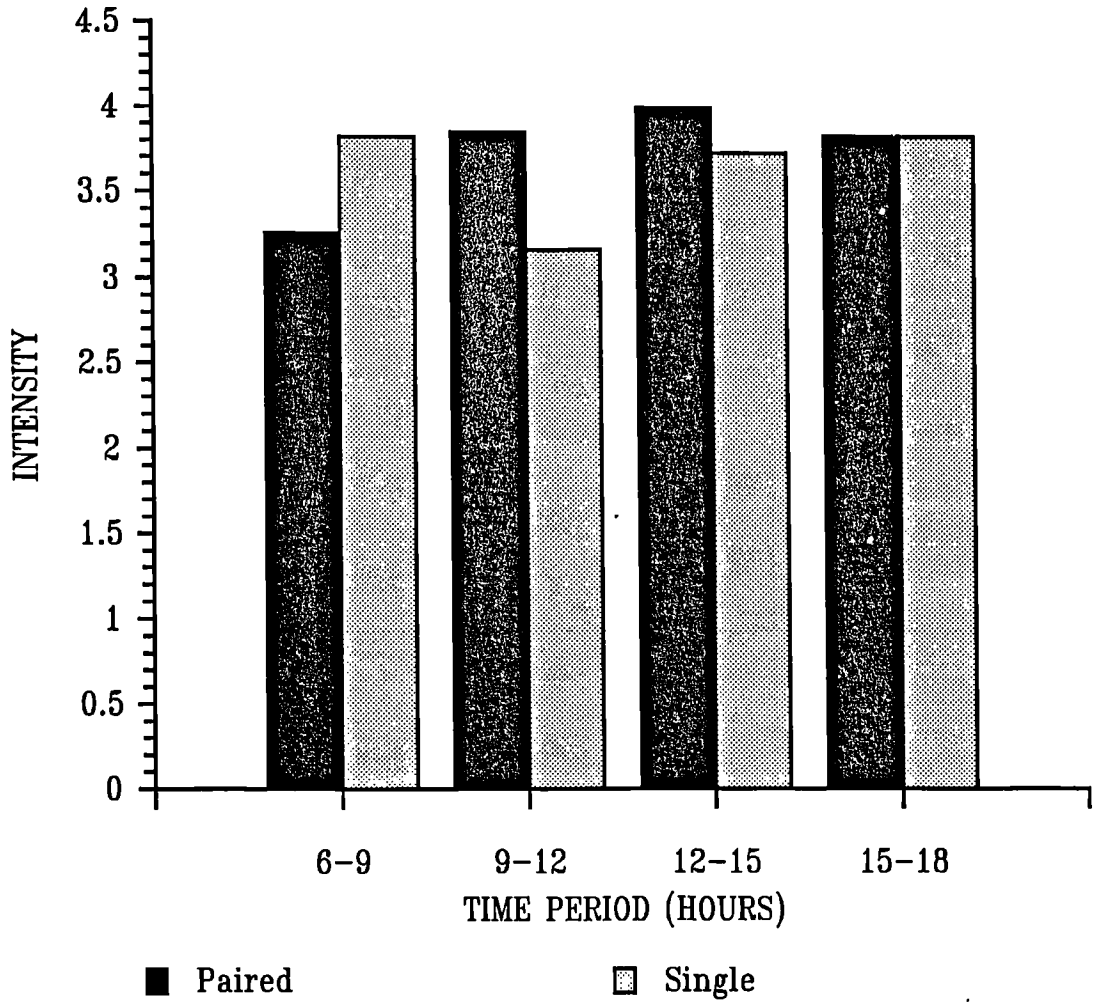

FIGURE 5.5. Change in the intensity of social interactions in paired and single male Ruddy Duck during the courtship period at MSWNR with time of day.

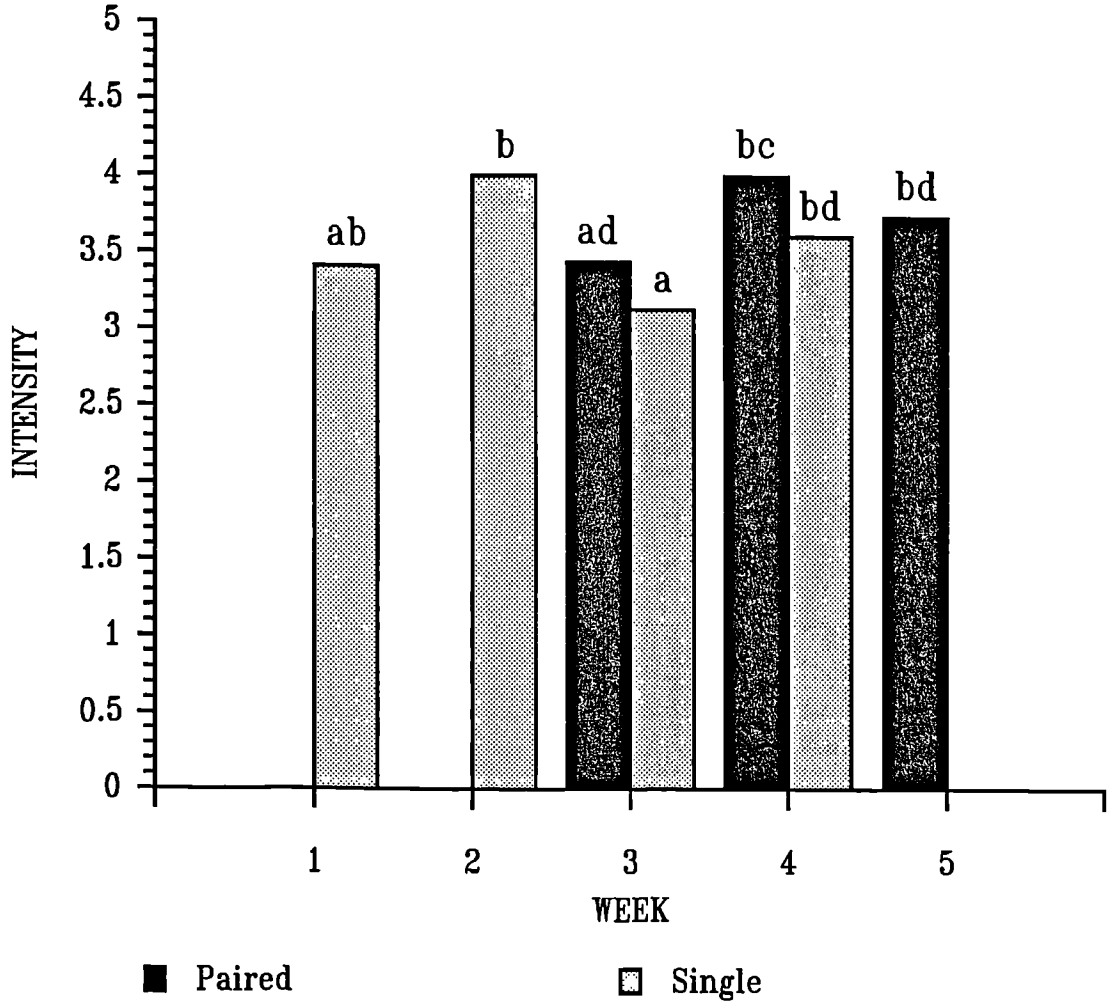

FIGURE 5.6. Change in the intensity of social interactions in paired and single male Ruddy Duck during the courtship period at MSWNR with date. Column means with different letters are significantly different (MW U-Tests, $p<0.05$).

5.4.3 Brood Females

5.4.3.1 Number of Interactions

5.4.3.1.1 Initial Considerations

Social interactions observed during the brood female time budget are summarised in Tables 5.6a and 5.6b. During the study there were a total of 1469 interactions involving five females in 134.0 hours of observation. The majority (63.3%) were intraspecific, all of which were initiated by the brood females. Females directed 50.4% (465/921) of intraspecific interactions (for which details of the species interacted with were recorded) towards the attending male Ruddy Duck. Most other intraspecific interactions were directed at other males (23.8%) or ducklings of other broods (20.3%). Interactions with other females constituted only 4.4% (39/921) of intraspecific interactions.

TABLE 5.6a. Intraspecific social interactions recorded during the brood female diurnal time budget at MSWNR. Number of hours of observation = 134.0. a - values calculated as a percentage of total interactions (intraspecific + interspecific) - see Table 5.6b.

Species	Initiated by Study Bird		Initiated by Other Bird		Not Recorded		Total	
	No.	% [a]	No.	%	No.	%	No.	%
Male - Attending	465	31.7	0	0	0	0	465	31.7
Male - Other	198	13.5	0	0	0	0	198	13.5
Male - Not recorded	21	1.4	0	0	0	0	21	1.4
Female	39	2.7	0	0	0	0	39	2.7
Duckling	187	12.7	0	0	0	0	187	12.7
Multiple	11	0.7	0	0	0	0	11	0.7
No details	9	0.6	0	0	0	0	9	0.6
TOTAL	930	63.3	0	0	0	0	930	63.3

Twenty species of bird and one species of mammal were involved in 519 interspecific interactions (for which details of the other species were recorded) with brood female Ruddy Ducks. Brood females initiated 93.6% (486/519) of interspecific interactions mainly against Mallard and Coot. Only Goldeneye initiated more interactions towards female Ruddy Ducks than female Ruddy Ducks initiated towards them. Great-crested

TABLE 5.6b. Interspecific social interactions recorded during the brood female diurnal time budget at MSWNR. Number of hours of observation = 134.0. a - values calculated as a percentage of total interactions (intraspecific + interspecific) - see Table 5.6a.

Species	Initiated by Study Bird		Initiated by Other Bird		Not Recorded		Total	
	No.	% [a]	No.	%	No.	%	No.	%
Little Grebe	15	1.0	4	0.3	0	0	19	1.3
Great-crested Grebe	25	1.7	11	0.7	1	0.1	37	2.5
Heron	7	0.5	0	0	0	0	7	0.5
Greylag Goose	3	0.2	0	0	0	0	3	0.2
Canada Goose	3	0.2	1	0.1	0	0	4	0.3
Shelduck	18	1.2	2	0.1	0	0	20	1.4
Gadwall	1	0.1	0	0	0	0	1	0.1
Teal	1	0.1	0	0	0	0	1	0.1
Mallard	144	9.8	0	0	0	0	144	9.8
Shoveler	1	0.1	0	0	0	0	1	0.1
Pochard	8	0.5	0	0	0	0	8	0.5
Tufted Duck	7	0.5	0	0	0	0	7	0.5
Goldeneye	2	0.1	6	0.4	0	0	8	0.5
Moorhen	30	2.0	0	0	0	0	30	2.0
Coot	136	9.3	1	0.1	0	0	137	9.3
Lapwing	25	1.7	1	0.1	0	0	26	1.8
Black-headed Gull	42	2.9	0	0	0	0	42	2.9
Lesser Black-backed Gull	9	0.6	5	0.3	0	0	14	1.0
Feral Pigeon	1	0.1	0	0	0	0	1	0.1
Blackbird	1	0.1	0	0	0	0	1	0.1
Rabbit	7	0.5	0	0	0	0	7	0.5
Multiple	1	0.1	0	0	0	0	1	0.1
No details	9	0.6	1	0.1	0	0	10	0.7
TOTAL	496	33.8	32	2.2	1	0.1	529	36.0
Species unknown	10	0.7	0	0	0	0	10	0.7
GRAND TOTAL	1436	97.8	32	2.2	1	0.1	1469	100.0

Grebes initiated most interactions (11) against females. Other species for which more

than ten interactions were observed were Little Grebe, Shelduck *Tadorna tadorna*, Moorhen, Lapwing *Vanellus vanellus*, Black-headed Gull and Lesser Black-backed Gull *Larus fuscus*.

A total of 1226 interactions (63.1% intraspecific, 36.9% interspecific) involving four brood females had no missing values and were included in further analysis.

Brood female Ruddy Ducks dominated most interspecific interactions with only six species winning interactions: Great-crested Grebe, Canada Goose, Pochard, Goldeneye, Coot and Lesser Black-backed Gull (Table 5.7). Brood females also showed a lower level of percentage wins against these species and Greylag Goose *Anser anser* compared with other species. Females won only 20% (1/5) of interactions with Goldeneye, 50% (4/8) with Pochard and 51.6% (16/31) with Great-crested Grebe. Nevertheless, the overall percentage of interactions won was 90.3% (408/452). The four interactions initiated by Goldeneye referred to one episode in which a brood female Goldeneye killed one four-day old duckling from the brood of female 1.

The distribution of the number of social interactions in which the four females were involved differed significantly from the expected distribution calculated from the total time of observation per female. Brood female 1 was involved in significantly more interactions than expected whilst female 3 was involved in significantly fewer (Table 5.8), hence the females were treated separately in further analyses.

Females 1, 3 and 4 were involved in 61.2-68.1% intraspecific interactions (Table 5.9) whilst female 2 was involved in noticeably fewer (48.0%). Brood females initiated 96.2-100% and won 97.2-100% of all interactions. Brood females initiated and won all intraspecific interactions whilst they initiated 89.7-100% of interspecific interactions and won 90.7-100% of those interspecific interactions where there was a clear winner.

5.4.3.1.2 Effect of Time of Day

Time of day had no significant effect on the number of social interactions involving females 1 and 2. Female 3 was involved in significantly fewer interactions than expected in late afternoon (Table 5.10) whilst female 4 was involved in significantly fewer at noon.

TABLE 5.7. Number of interspecific social interactions and percentage wins of brood female Ruddy Duck at MSWNR.

Species	Won by Female		No Clear Winner		Won by Other Species		Total
	No.	%	No.	%	No.	%	No.
Little Grebe	9	100.0	0	-	0	-	9
Great-crested Grebe	16	51.6	12	38.7	3	9.7	31
Heron	6	85.7	1	14.3	0	-	7
Greylag Goose	2	66.7	1	33.3	0	-	3
Canada Goose	2	50.0	1	25.0	1	25.0	4
Shelduck	18	100.0	0	-	0	-	18
Gadwall	1	100.0	0	-	0	-	1
Teal	1	100.0	0	-	0	-	1
Mallard	136	99.3	1	0.7	0	-	137
Shoveler	1	100.0	0	-	0	-	1
Pochard	4	50.0	2	25.0	2	50.0	8
Tufted Duck	7	100.0	0	-	0	-	7
Goldeneye	1	20.0	0	-	4	80.0	5
Moorhen	27	100.0	0	-	0	-	27
Coot	110	92.4	4	3.4	5	4.2	119
Lapwing	25	96.2	1	3.8	0	-	26
Black-headed Gull	36	97.3	1	2.7	0	-	37
Lesser Black-backed Gull	5	50.0	0	-	5	50.0	10
Feral Pigeon	1	100.0	0	-	0	-	1
Blackbird	1	100.0	0	-	0	-	1
Rabbit	7	100.0	0	-	0	-	7
All Interactions	408	90.3	24	5.3	20	4.4	452

5.4.3.1.3 Effect of Age of Brood

All brood females were involved in fewer interactions than expected while accompanying older ducklings (Table 5.11), significantly so in females 1 and 4. Females 1, 2 and 4 were involved in more interactions than expected while accompanying ageclass 1 ducklings, but not significantly so. Similarly, females 1, 2 and 4 all showed a decreasing rate of social interaction with increasing duckling ageclass (Fig. 5.7). In contrast, female

TABLE 5.8. Comparison of the number of social interactions involving individual brood female Ruddy Duck at MSWNR.

Brood Female	Number of Interactions	Observed %	Expected %	Difference	Significance
1	370	30.18	15.71	MORE	$p < 0.001$
2	252	20.55	22.72	LESS	NS
3	250	20.39	32.40	LESS	$p < 0.001$
4	354	28.87	29.17	LESS	NS

TABLE 5.9. Social interactions involving individual brood female Ruddy Duck at MSWNR.

Brood Female	Number of Interactions	% Initiated by		% Won by		% Intra-specific	% Inter-specific
		Female	Other Species	Female	Other Species		
1	370	96.2	3.8	97.2	2.8	67.8	32.2
2	252	98.0	2.0	100	0	48.0	52.0
3	250	100	0	98.8	1.2	61.2	48.8
4	354	97.5	2.5	97.7	2.3	68.1	31.9

3 was involved in significantly less interactions than expected while accompanying ageclass 1 ducklings. Only female 1 showed a significant negative correlation between the rate of social interaction (expressed as the mean rate of interaction per day of duckling age) and duckling ageclass (r_s=-0.568, n=15, $p<0.05$).

5.4.3.2 Duration of Interactions

5.4.3.2.1 Initial Considerations

Examination of probability plots showed that the data approximated to normal after log-transformation, therefore parametric statistics were employed when the log-transformed data met the other assumptions of the analysis.

Length of interaction differed significantly between brood females and between intra- and interspecific interactions (two-way ANOVA, $p<0.05$). There was also a significant

TABLE 5.10. Changes in the number of social interactions of brood female Ruddy Duck at MSWNR with time of day.

Time of Observation	Number of Interactions	Observed %	Expected %	Difference	Significance
Female 3					
Early Morning (0400 - 0659)	43	17.20	14.00	MORE	NS
Mid Morning (0700 - 0959)	55	22.00	15.49	MORE	NS
Noon (1000 - 1259)	59	23.60	19.25	MORE	NS
Early Afternoon (1300-1559)	26	10.40	13.57	LESS	NS
Late Afternoon (1559 - 1859)	32	12.80	19.66	LESS	$p < 0.05$
Evening (1900 - 2159)	35	14.00	18.04	LESS	NS
Female 4					
Early Morning (0400 - 0659)	34	9.60	11.94	LESS	NS
Mid Morning (0700 - 0959)	65	18.36	16.47	MORE	NS
Noon (1000 - 1259)	35	9.89	15.25	LESS	$p < 0.05$
Early Afternoon (1300-1559)	82	23.16	17.72	MORE	NS
Late Afternoon (1559 - 1859)	53	14.97	18.69	LESS	NS
Evening (1900 - 2159)	85	24.01	19.93	MORE	NS

interaction between these two variables, therefore intra- and interspecific interactions were treated separately for each brood female in further analyses. Interspecific interactions were longer than intraspecific interactions in all brood females, significantly so in females 1, 2 and 4 (Table 5.12).

Brood female 1 was involved in significantly longer intraspecific interactions than the other three females whilst female 2 was involved in significantly longer intraspecific interactions than female 4. Brood females 1 and 2 were involved in significantly longer

TABLE 5.11. Changes in the number of social interactions of brood female Ruddy Duck at MSWNR with brood ageclass.

	Number of Interactions	Observed %	Expected %	Difference	Significance
Female 1					
Ageclass 1	88	23.78	18.67	MORE	NS
2	125	33.78	29.85	MORE	NS
3	157	42.43	51.48	LESS	$p < 0.01$
Female 2					
Ageclass 1	108	42.86	39.07	MORE	NS
2	144	57.14	58.17	LESS	NS
Female 3					
Ageclass 1	11	4.40	8.79	LESS	$p < 0.05$
2	140	56.00	50.06	MORE	NS
3	99	39.60	41.15	LESS	NS
Female 4					
Ageclass 1	103	29.10	23.31	MORE	NS
2	149	42.09	41.06	MORE	NS
3	95	26.84	25.59	MORE	NS
4	7	1.98	10.04	LESS	$p < 0.001$

TABLE 5.12. Interaction duration of brood females at MSWNR. Means in the same row or column with different letters are significantly different (MW U-Tests, $p<0.05$).

Brood Female	Length of interaction (Secs)					
	Intraspecific			Interspecific		
	N	Mean	S.E.	N	Mean	S.E.
1	251	3.98 a	0.152	119	7.74 c	0.763
2	121	3.32 b	0.246	131	5.72 c	0.391
3	153	3.28 bc	0.248	97	3.49 b	0.568
4	241	2.87 c	0.162	113	3.52 b	0.259

interspecific interactions than females 3 and 4.

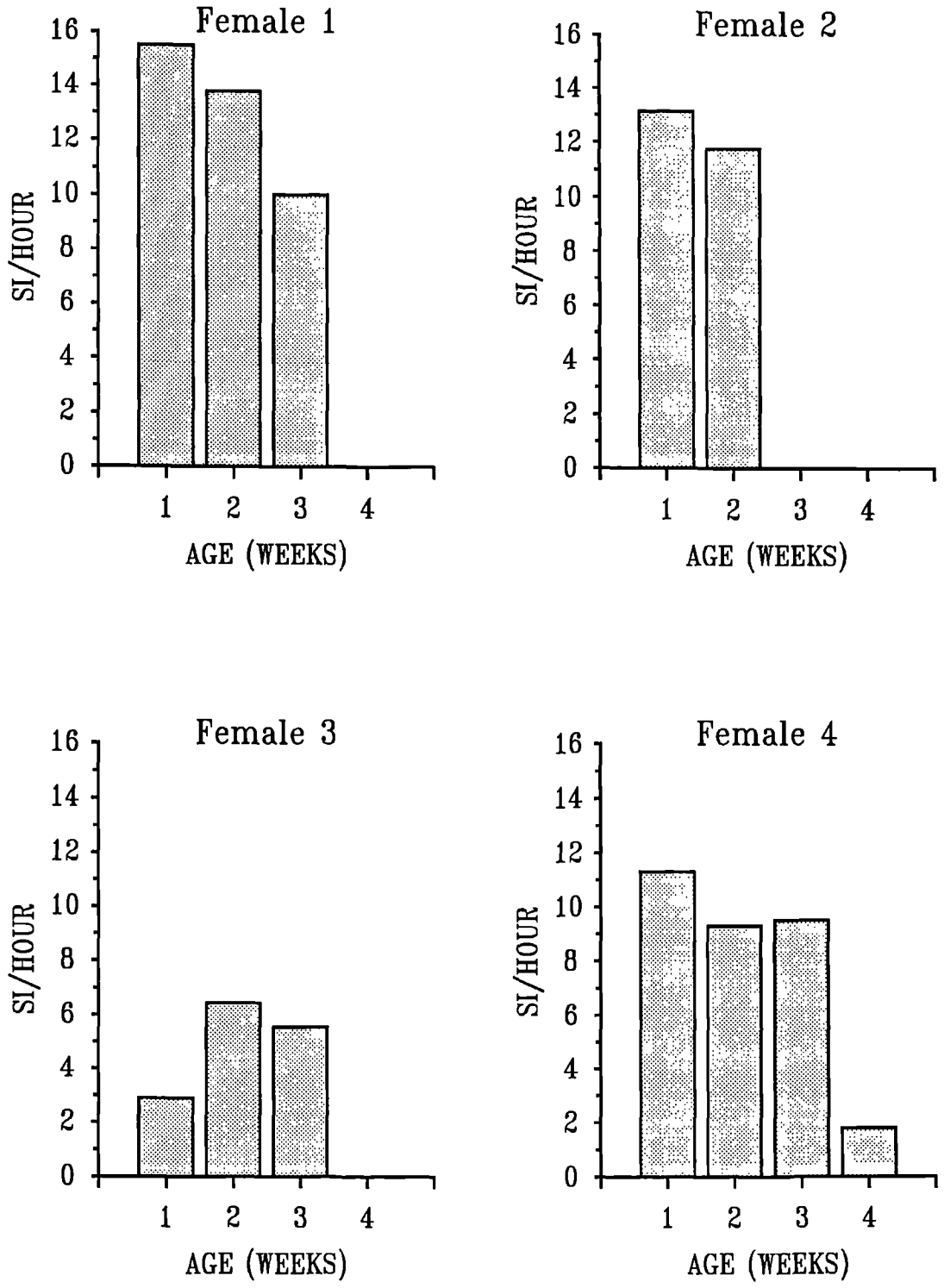

FIGURE 5.7. Change in the rate of social interaction in brood female Ruddy Duck at MSWNR with brood age.

5.4.3.2.2 Effect of Time of Day

The duration of intraspecific social interactions involving brood female Ruddy Ducks remained relatively constant throughout the day (Fig. 5.8). Only female 2 showed any significant difference in interaction duration between time periods (ANOVA, $p<0.001$) with longer interactions in the early afternoon period than at any other time of day.

The duration of interspecific interactions did not differ significantly between time periods for any brood female (KW Tests, $p>0.05$).

5.4.3.2.3 Effect of Age of Brood

Interactions involving females with ageclass 4 broods were excluded from the analysis because of a small sample size. Intraspecific interaction duration did not differ between brood ageclasses for any brood female (ANOVA's, $p>0.05$), although female 1 showed a significant (though slight) positive correlation between brood age and interaction duration ($r_p=0.161$, $N=251$, $p<0.01$) and female 4 showed a significant (though slight) negative correlation ($r_p=-0.136$, $N=239$, $p<0.05$).

The duration of interspecific interactions did not differ significantly between ageclasses (ANOVA's, $p>0.05$) and there were no significant correlations between interspecific interaction duration and brood age for any brood female (Pearson's correlations, $p>0.05$).

5.4.3.3 Intensity of Interactions

5.4.3.3.1 Initial Considerations

A total of 1198 interactions (63.9% intraspecific, 36.1% interspecific) were initiated by females and included in the analysis. Hunched Rushes constituted 54.8% and Open-billed Threats 29.6% of the interactions (Table 5.13) with much lower proportions of low intensity ("Swam At" and Hunched Threat) and high intensity (Physical Contact) interactions.

Interaction intensity differed significantly between brood females. Female 3 had significantly lower interaction intensities than the other females (MW U-Tests, $p<0.05$). This was mainly caused by higher levels of low intensity "Swam At" and Hunched Threat behaviours. Female 1 also showed noticeably higher levels of "Swam At" interactions

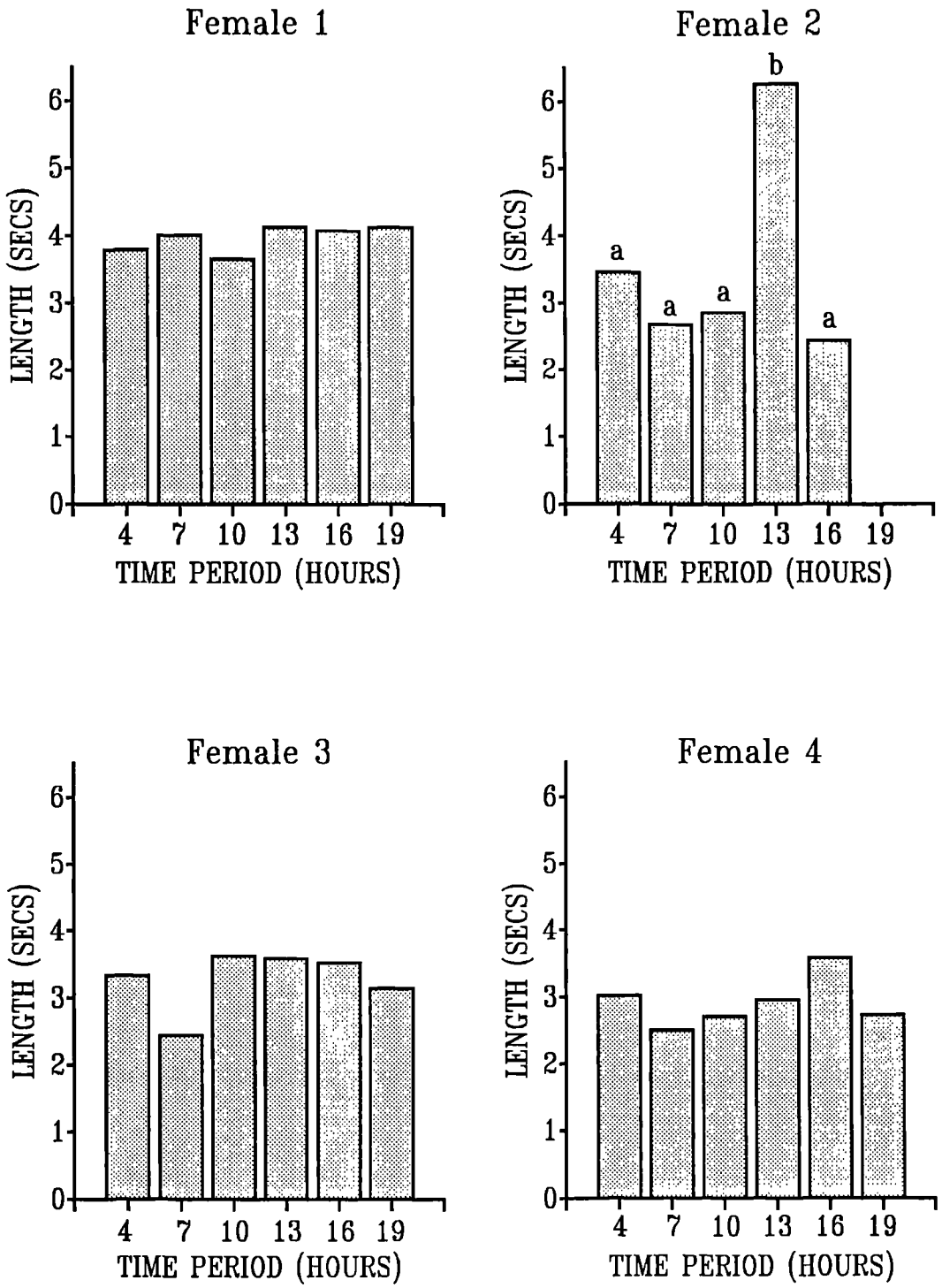

FIGURE 5.8. Change in the duration of intraspecific interactions in brood female Ruddy Duck at MSWNR with time of day. Column means with different letters are significantly different (MW U-Tests, $p<0.05$).

TABLE 5.13. Intensity of interactions of brood female Ruddy Duck at MSWNR.

Intensity	No. of Interactions (% per female)				
	Female 1	Female 2	Female 3	Female 4	All Birds
1. Swam at	35 (9.8)	0	30 (12.0)	6 (1.7)	71 (5.9)
2. Hunched Threat	5 (1.4)	5 (2.0)	41 (16.4)	33 (9.6)	84 (7.0)
3. Open-billed Threat	105 (29.5)	105 (42.5)	61 (24.4)	84 (24.3)	355 (29.6)
4. Hunched Rush	203 (57.0)	131 (53.0)	116 (46.4)	206 (59.7)	656 (54.8)
5. Physical contact	8 (2.3)	6 (2.4)	2 (0.8)	16 (4.6)	32 (2.7)
Total	356	247	250	345	1198

than females 2 and 4.

Interspecific interactions were of significantly higher intensity than intraspecific interactions (MW U-Test, $p<0.05$), therefore intra- and interspecific interactions for each brood female were treated separately in further intensity analyses.

5.4.3.3.2 Effect of Time of Day

The intensity of intraspecific social interactions initiated by brood female Ruddy Ducks remained relatively constant throughout the day (Fig. 5.9). The only notable change in intraspecific interaction intensity was that females tended to initiate less intense interactions in the afternoon and evening, significantly so in females 1 and 2.

There was no difference in interspecific interaction intensity with time of day in three of the females (Fig. 5.10). Female 2 initiated significantly less intense interspecific interactions during the noon time period than in late morning and afternoon.

5.4.3.3.3 Effect of Age of Brood

Interactions initiated by females with ageclass 4 broods were excluded from the analysis because of the small sample size. Intraspecific interaction intensity decreased with increasing duckling age in females 1, 2 and 3, significantly so in female 3 ($r_s=-0.210$, $n=153$, $p<0.01$). Female 3 also initiated significantly less intense interactions while accompanying ageclass 3 than ageclass 2 ducklings (Fig. 5.11).

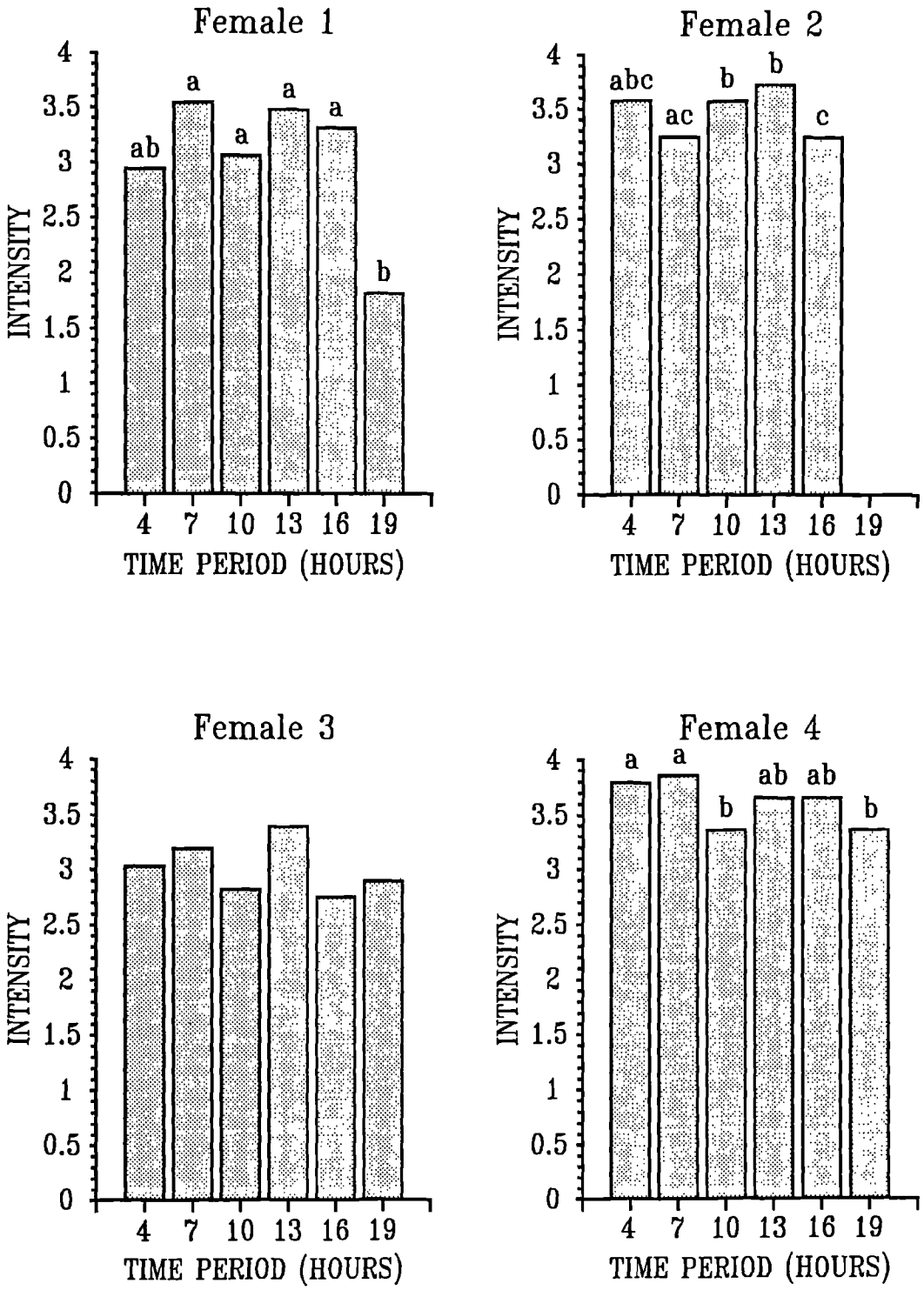

FIGURE 5.9. Change in the intensity of intraspecific interactions in brood female Ruddy Duck at MSWNR with time of day. Column means with different letters are significantly different (MW U-Tests, $p<0.05$).

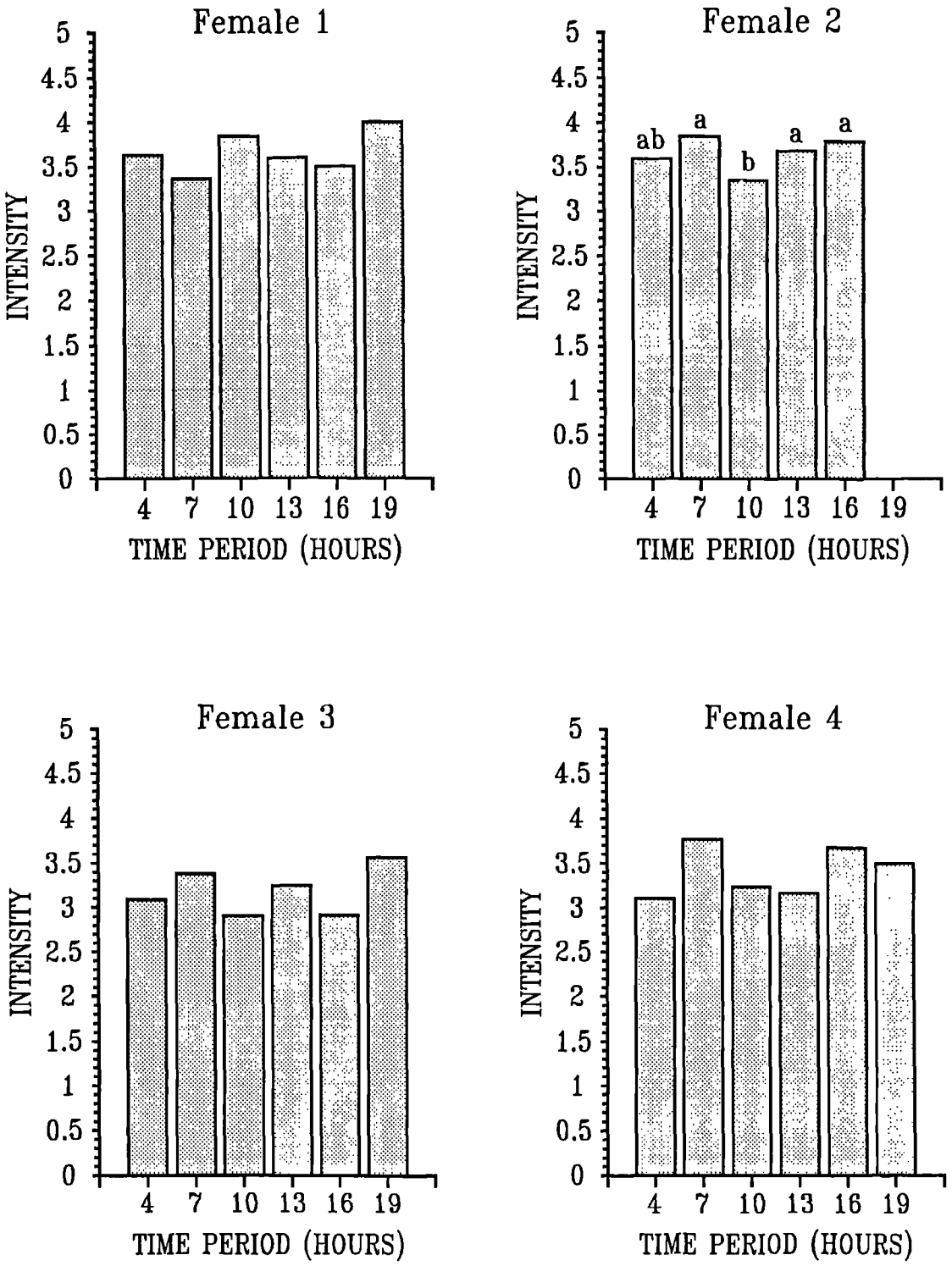

FIGURE 5.10. Change in the intensity of interspecific interactions in brood female Ruddy Duck at MSWNR with time of day. Column means with different letters are significantly different (MW U-Tests, $p<0.05$).

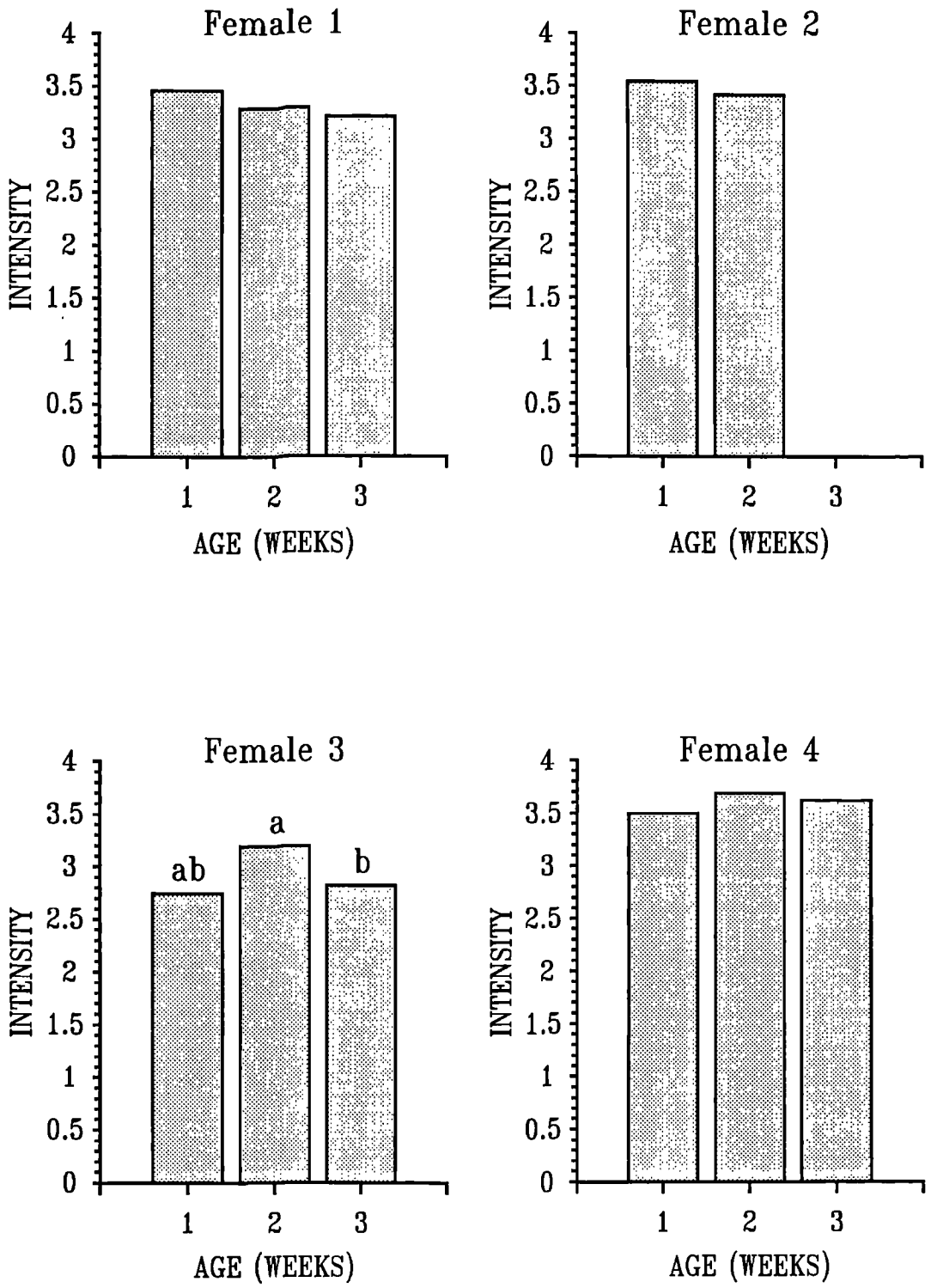

FIGURE 5.11. Change in the intensity of intraspecific interactions in brood female Ruddy Duck at MSWNR with brood ageclass. Column means with different letters are significantly different (MW U-Tests, $p<0.05$).

Interspecific interaction intensity decreased with increasing duckling age in females 1, 2 and 4, significantly so in female 2 (r_s=-0.294, n=126, p<0.001). Female 2 also initiated significantly less intense interactions while accompanying ageclass 2 than ageclass 1 ducklings (Fig. 5.12).

5.4.4 Rate of Social Interaction

Tables 5.14, 5.15, 5.16a and 5.16b, 5.17 and 5.18 summarise the rate of social interaction in wintering dabbling ducks, Canvasback during spring migration, Ruddy Ducks, wintering diving ducks and ducks and coot during the breeding season, respectively. These tables are located in the discussion section where their contents are considered. Note that the figures provide only a basic comparison of the rates of social interaction, as they may not be directly comparable due to variation, firstly, in sample size and length of observation and, secondly, in uncontrollable variables, such as the density and aggressiveness of conspecifics and other species present.

5.5 DISCUSSION

This discussion is divided into three sections. The first two deal with the detailed analyses of the social interactions of courting male and brood female Ruddy Ducks. The third is a comparative discussion of the social interactions of Ruddy Ducks throughout the year with consideration of their effect on native waterbirds in Great Britain.

5.5.1 Courting Male Social Interaction

5.5.1.1 Effect of Time of Day

Single male Ruddy Ducks were involved in more interactions than expected and paired males in longer interactions in the evening period. These facts will probably be related to the increased level of courtship display which male Ruddy Ducks show in the evening (see Chapter Three). This aside, social interactions in courting male Ruddy Ducks showed very little variation in number, duration or intensity with time of day.

5.5.1.2 Effect of Date/Pairing Status

As may have been expected, given that most of the interactions included in the analysis

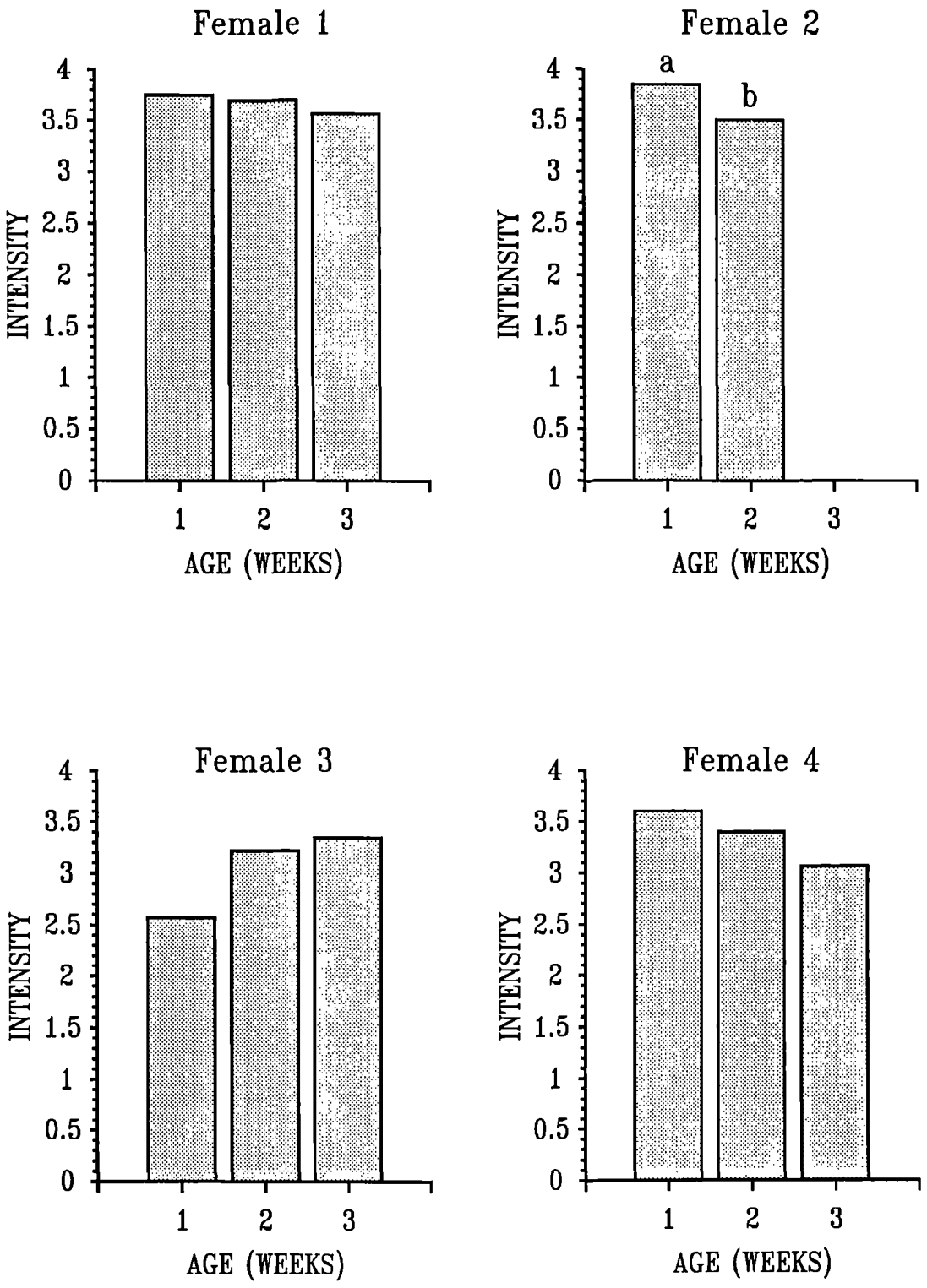

FIGURE 5.12. Change in the intensity of interspecific interactions in brood female Ruddy Duck at MSWNR with brood ageclass. Column means with different letters are significantly different (MW U-Tests, $p<0.05$).

were intraspecific and initiated by males, the level of social interaction in courting male Ruddy Ducks depended mainly on date and pairing status. Paired male Ruddy Ducks initiated and won a significantly higher proportion of interactions than single males, reflecting their higher dominance rank. Similarly, in California, paired male Ruddy Ducks showed a significantly higher rate of aggressive display than single males during the pre-nesting period and won 80% of 74 encounters with single males (Gray 1980). At MSWNR, paired males were involved in significantly longer interactions than single birds, but interaction intensity did not differ. If data presented in Gray (1980) are reanalysed to investigate the intensity of interaction, there were no significant differences in the intensity of interactions between paired and single males in her study, either in the pre-nesting period only or in the breeding season as a whole (MW U-Tests, $p>0.05$). These results may suggest that the number and duration of interactions provide a measure of dominance in courting male Ruddy Ducks while interaction intensity is less useful in this respect. However, it would be necessary to compare the dominance rank of individual males with the number, duration and intensity of interactions to substantiate this suggestion.

Dominance of paired over unpaired birds has been noted in many other waterfowl, for example, Bewick's Swan *Olor columbianus bewickii* (Scott 1980), Shelduck (Patterson 1982), Gadwall (Paulus 1983), North American Black Duck (Hepp 1989), Canvasback (Lovvorn 1990), Eider (Ashcroft 1976) and Goldeneye (Afton and Sayler 1982). Paired Gadwall also showed a higher rate of foraging aggression than single birds (Table 5.14). In contrast, paired male Canvasback on spring migration did not show consistently higher rates of foraging or courtship aggression than single males (Lovvorn 1990), but the small sample sizes for paired males in this study limits this interpretation (Table 5.15).

To reemphasize the changes in behaviour which occurred in courting male Ruddy Ducks during the courtship period, paired males were first observed at MSWNR on 2 April 1989 or week 3 of the study. The number of interactions involving single males was significantly higher than expected in week 2 and there was a non-significant increase in the duration and intensity of interactions between weeks 1 and 2. In week 3, paired males showed a significantly higher level of interaction than expected whilst both paired and single males showed a decrease in interaction intensity from week 2. Paired males were then involved in significantly fewer interactions than expected in week 4, however, they

TABLE 5.14. Rate of social interaction in wintering dabbling ducks.

Species	Reference	Study Period	Age/sex Class	Type of Interaction	Total Number of Interactions	Length of Observation (Hrs)	Rate of Interaction (SI/hour)
Gadwall	Paulus (1983)	Oct 1977 - Apr 1978	All	All	601	231	2.60
				Interspecific	87	231	0.38
				Intraspecific	514	231	2.23
			Paired Birds	Intra- and Interspecific - mainly intraspecific foraging aggression	437	231	1.89
			Single Males		57	231	0.25
			Single Females		61	231	0.26
American Wigeon	Hepp and Hair (1984)	Nov-Feb 1978-80	All	Intraspecific	86	35.9	2.40
Gadwall					154	67.8	2.27
Green-winged Teal					351	69.2	5.07
North American Black Duck					107	54.9	1.95
Pintail					223	62.9	3.54
Shoveler					206	63.8	3.23

TABLE 5.15. Rate of intraspecific social interaction in Canvasback during spring migration (from Lovvorn 1990). a - data collected March-April 1984. b - data collected March-April 1983.

Study Site	Age/sex Class	Type of Interaction	Total Number of Interactions	Length of Observation (Hrs)	Rate of Interaction (SI/hour)
Long Point Bay, Ontario [a]	Paired Males	Foraging Aggression	4	2.4	1.56
	Single Males		134	32.8	4.08
	Paired Females		13	5.6	2.40
	Single Females		101	28.1	3.60
Mississippi River, Wisconsin [b]	Paired Males	Foraging Aggression	23	2.0	11.40
	Single Males		199	23.4	8.52
	Paired Females		35	4.3	8.16
	Single Females		78	11.4	6.84
Long Point Bay, Ontario [a]	Paired Males	Courtship Aggression	0	2.4	0
	Single Males		8	32.8	0.24
	Paired Females		126	5.6	22.56
	Single Females		216	28.1	7.68
Mississippi River, Wisconsin [b]	Paired Males	Courtship Aggression	1	2.0	0.48
	Single Males		11	23.4	0.48
	Paired Females		18	4.3	14.16
	Single Females		93	11.4	8.16

were involved in significantly longer interactions than single males. Both paired and single males were involved in interactions of significantly higher intensity in week 4 than in week 3. In week 5, single males were involved in significantly fewer interactions than expected whilst the length of interactions involving paired males continued to increase.

These results can be explained in terms of the reproductive strategies employed by male Ruddy Ducks, given that there is an excess of males at MSWNR. During courtship, male Ruddy Ducks usually form courting parties, the males in which then either display *en masse* to females or display to one another in the absence of females. This communal display is important in establishing the dominance hierarchy which is typical of stifftail males during the breeding season (e.g. Siegfried 1985; Marchant and Higgins 1990). While the dominance hierarchy is in the process of being established, that is, as the courtship period progresses towards pair formation, the level of courtship activity increases. Once the dominant males are paired (in week 3 of this study), they defend their newly acquired mates constantly and are involved in more interactions than expected, but because the dominance hierarchy among familiar males is already established, defensive interactions need only be of low intensity.

Once pair bonds are fully established (in week 4), paired males are involved in fewer, longer interactions, of a higher intensity than earlier. This reflects their dominance plus their increased commitment to defend their mates. Paired male North American Black Ducks showed a similar increase in intraspecific interaction intensity as the breeding season progressed towards egg-laying (Seymour and Titman 1979). The higher intensity of interaction in single males in week 4 compared with the previous week could be explained in terms of them being involved in interactions with paired males in an increased attempt to obtain an already paired bird as a mate. The fact that paired males are involved in significantly longer interactions than single males in week 4 may also be an indication of the higher dominance rank of paired birds. Given that the majority of interactions were intraspecific, involved males and that there was an excess of paired males, it is more likely that an interaction involving a subordinate single bird would be concluded more quickly than that involving a dominant paired bird. By week 5, single male Ruddy Ducks had failed to acquire a mate and were involved in significantly fewer interactions than expected.

The significant positive correlation between interaction duration and week of the study period in paired males may be another indication of their increasing commitment to the defence of their mates.

5.5.2 Brood Female Social Interaction

5.5.2.1 Inter-female Difference in Level of Social Interaction

The number, duration and intensity of interaction differed significantly between brood females. Female 1 was involved in significantly more interactions than expected which were of a significantly longer duration than in the other females whilst female 3 was involved in significantly fewer interactions than expected which were of a significantly lower intensity than in the other females. This may be construed as being caused by a difference in the level of individual aggression, female 1 being the most aggressive and female 3 the least. The fact that female 1 was the only bird to initiate a relatively high proportion of interactions against Lapwing on the pool margins may support this contention. However, there are a number of other factors which may be important, some of which will also be related to the level of parental care and alert behaviour exhibited by the females (see Chapter Four).

The density of conspecifics and other species present on brood-rearing areas will be related to the level of social interaction, in that a higher density of individuals will lead to a higher probability of encounter and hence a higher level of social interaction. This will be combined with the level of aggression shown by other birds present which, in turn, will be affected by their age, sex, pairing and breeding status. In a given species, brood-rearing females will tend to be dominant (e.g. this study) while adults will be dominant over first year birds (e.g. Alexander 1987; Hepp 1989), males over females (e.g. Choudhury and Black 1991) and paired birds over single birds (see section 5.5.1.2). Such a dominance hierarchy will exist for all species present and the relative proportions of each "dominance" class in each species will affect the probability of interaction. Habitat characteristics also affect the level of aggression in brood female Ruddy Ducks. Females on large lakes appeared to be less aggressive, both in terms of the number and intensity of interaction, than birds on enclosed canals (Joyner 1977).

The collection of such details for all species present was not possible during this study.

However, the presence/absence of certain species during the two years of this study may have affected the results considerably. In particular, the presence of brood-rearing Great-crested Grebes on the Washing Well in 1988 (affecting females 1 and 2) may partially explain the higher level of interaction observed in female 1. The presence of Ruddy ducklings from other broods also influenced the level of interaction. Brood females threatened Ruddy ducklings from other broods by simply swimming at them. No ducklings were present during the brood-rearing periods of females 2 and 4, whereas the offspring of these females were present during brood-rearing in females 1 and 3, hence the higher occurrence of "Swam At" behaviour in the latter two females. The presence of attending or displaying males caused an increase in the level of interaction. In fact, the contrasting levels of interaction in females 1 and 3 can probably be best explained in this way. Female 3 was accompanied by a male only intermittently and was involved in no interactions with other males, whereas female 1 was accompanied on most days and involved in many interactions with other males.

Potential predators of ducklings, such as Lesser Black-backed Gulls and Herons *Ardea cinerea*, also affected the level of interaction. As no predation attempts were observed, the actual effect of gull presence was to induce a higher number of longer, medium intensity interactions, mainly Open-billed Threats.

Most intraspecific interactions of brood females at MSWNR and in Utah (Joyner 1977) were directed at males whilst 33% of interactions in Utah were directed at females compared to only 4.4% at MSWNR. This will probably be caused by the higher number of breeding females in Utah.

5.5.2.2 Effect of Time of Day

Time of day had relatively little effect on the number, duration or intensity of interactions of brood female Ruddy Ducks. Certainly, there were no consistent fluctuations in the number, duration or intensity of interactions for individual females or between females with time of day. This may be expected considering that time of day had little effect on the time budget of brood female Ruddy Ducks at MSWNR (see Chapter Four).

5.5.2.3 Effect of Date/Brood Age

The number and intensity of interactions initiated by brood female Ruddy Ducks tended

to decrease with increasing brood age, although there was individual variation between females. Brood age had no consistent effect on interaction duration. The decrease in the number of interactions with brood ageclass was most apparent in female 1 which was involved in significantly more interactions than expected and may be construed as being the most aggressive. Given that the level of parental care in brood female Ruddy Ducks tends to decrease with increasing brood age (see Chapter Four), a decrease in social interaction would be expected as the brooding drive of the females waned towards the point of brood desertion. Joyner (1977) also noted that the aggressive behaviour of brood female Ruddy Ducks decreased with increasing brood age and Savard (1982) made similar observations of brood female Barrow's Goldeneye *Bucephala icelandica*.

5.5.3 Seasonal Variation in Social Interaction

Ruddy Ducks were studied during the three major portions of the annual cycle when social interaction may have been expected: the winter or non-breeding season, the courtship period and the brood-rearing period. The rate of intra- and interspecific social interaction is compared between these periods. However, note that although a high rate of interaction may imply a high level of aggression, it does not necessarily imply dominance.

5.5.3.1 Intraspecific Interaction

The majority of Ruddy Duck social interactions were intraspecific at all times of the year. The rate of intraspecific interaction was lowest in winter (Table 5.16) when birds were highly gregarious, feeding and loafing in large flocks with little aggression. Similarly, Bergan and Smith (1989) recorded no intraspecific interactions during 72.4 hours of observation of Ruddy Ducks wintering on a reservoir in South Carolina. In the same study, Bufflehead and Lesser Scaup had very low levels of interaction, whereas there was a slightly higher level in Ring-necked Duck (Table 5.17a). Gadwall wintering in Louisiana (Paulus 1983), American Wigeon, Gadwall, Green-winged Teal, North American Black Duck, Pintail and Shoveler wintering in North Carolina (Hepp and Hair 1984), Canvasback, Redhead, Ring-necked Duck and Lesser Scaup wintering in coastal South Carolina (Alexander 1987) and paired male Barrow's Goldeneye wintering in coastal British Columbia (Savard and Smith 1987) all showed even higher rates of intraspecific interaction (Tables 5.14, 5.17a and 5.17b). Paired female Barrow's

TABLE 5.16. Rate of Ruddy Duck social interaction. a - includes 6 interactions with unknown species. b - includes 1 interaction with an unknown species. a - includes 10 interactions with unknown species.

Reference	Time of Year	Age/sex Class	Type of Interaction	Total Number of Interactions	Length of Observation (Hrs)	Rate of Interaction (SI/hour)
Bergan (1986)	Winter (Jan-Apr 1985, Nov 1985-Mar 1986)	All	All	11	72.4	0.15
			Interspecific	11	72.4	0.15
This study	Winter (Jan-Feb 1988)	All	All	75 [a]	124.6	0.60
			Interspecific	23	124.6	0.18
			Intraspecific	46	124.6	0.37
This study	Spring (Mar-Apr 1989)	Courting Males	All	255 [b]	111.3	2.29
			Interspecific	17	111.3	0.15
			Intraspecific	237	111.3	2.13
Gray (1980)	Spring/Summer (May-Jul 1975-76)	Males	All	508	134.6	3.77
	Pre-nesting Period			86	40.9	2.10
	Nesting Period			275	56.7	4.85
	Hatching Period			147	37.0	3.97
This study	Summer (Jun-Jul 1988/89)	Brood Females	All	1469 [c]	134.0	10.96
			Interspecific	529	134.0	3.95
			Intraspecific	930	134.0	6.94
Joyner (1977)	Summer (May-Aug 1972-74)	Brood Females	Interspecific	163	26.0	6.27
			Intraspecific	102	24.0	4.25

TABLE 5.17a. Rate of social interaction in wintering diving ducks.

Species	Reference	Study Period	Age/sex Class	Type of Interaction	Total Number of Interactions	Length of Observation (Hrs)	Rate of Interaction (SI/hour)
Ring-necked Duck	Bergan (1986)	Jan-Apr 1985, Nov 1985 - Mar 1986	All	All	62	104.7	0.59
				Interspecific	6	104.7	0.06
				Intraspecific	56	104.7	0.53
Lesser Scaup				All	12	111.6	0.11
				Interspecific	1	111.6	0.01
				Intraspecific	11	111.6	0.10
Bufflehead				All	7	95.2	0.07
				Interspecific	5	95.2	0.05
				Intraspecific	2	95.2	0.02
Barrow's Goldeneye	Savard and Smith (1987)	Winter 1982 + 1983	Paired Males	All	247	28	8.82
				Interspecific	79	28	2.82
				Intraspecific	168	28	6.00
			Paired Females	All	21	28	0.75
				Interspecific	6	28	0.21
				Intraspecific	15	28	0.54

TABLE 5.17b. Rate of social interaction in wintering diving ducks (from Alexander 1987). Data refers to all age/sex classes combined, collected November-March, 1975-1977.

Species	Type of Interaction	Total Number of Interactions	Length of Observation (Hrs)	Rate of Interaction (SI/hour)
Canvasback	All	1993	136.6	14.59
	Interspecific	655	136.6	4.80
	Intraspecific	1338	136.6	9.80
Redhead	All	603	37.7	15.99
	Interspecific	399	37.7	10.58
	Intraspecific	204	37.7	5.41
Ring-necked Duck	All	1269	120.1	10.57
	Interspecific	536	120.1	4.46
	Intraspecific	733	120.1	6.10
Lesser Scaup	All	941	65.3	14.41
	Interspecific	492	65.3	7.53
	Intraspecific	449	65.3	6.88

Goldeneye showed the lowest rate of interaction in winter as winter territorial behaviour in this species was primarily the rôle of the male. Canvasback, in which dominant males defended optimal feeding territories, exhibited the highest.

During winter, Ruddy Ducks appear to be one of the least aggressive species of anatid. This results from a low level of foraging aggression, a lack of territorial behaviour and the fact that courtship display, the development of the male social hierarchy and subsequent pair formation occur on the breeding grounds thus presenting minimal social stimuli for intraspecific interaction.

After arrival on the breeding grounds the rate of intraspecific social interaction in male Ruddy Ducks increases to nearly six times the winter level. At first, most is related to communal courtship display, the development of the male social hierarchy and competition for mates. Later, following pair formation, much social interaction in paired males is concerned with mate defence while single males struggle to acquire an already-paired female as a mate.

Gray (1980) presented data on the agonistic interactions of male Ruddy Ducks throughout the breeding season, but did not state if these data referred to intraspecific interactions, interspecific interactions or both. Assuming all interactions were included, male Ruddy Ducks during the pre-nesting period in California showed a similar rate of social interaction to courting males at MSWNR (Table 5.16). The rate of social interaction in both paired and single male Ruddy Ducks in California increased from the pre-nesting period to the nesting period then remained high during brood-rearing. This probably reflects the increased investment of paired birds in the defence of their mates, but further explanation is difficult because Gray did not state the percentage of encounters initiated by focal individuals or provide details of the species with which interactions occurred.

The rate of intraspecific interaction in courting male Ruddy Ducks at MSWNR was reasonably similar to the rate of intraspecific foraging aggression, but much higher than the rate of courtship aggression, in male Canvasback on spring migration in Ontario (Lovvorn 1990). This higher rate of courtship aggression in male Ruddy Ducks will be caused, not only by the highly competitive nature of their communal courtship, but also by the fact that male Ruddy Ducks, unlike male Canvasback, take a major rôle in repelling the courtship advances of other males.

During the courtship period, interactions were usually won by birds which initiated them. Although most of these interactions were initiated by alternate males, the fact that basic males and females won all encounters initiated against alternate males suggests that the interaction initiator was usually dominant, regardless of sex or plumage category. Similarly, Lovvorn (1990) found that in Canvasback the majority of intraspecific interactions during foraging aggression were won by the initiator, regardless of age or pairing status.

Interactions initiated by paired female Ruddy Ducks against their mates during the courtship period were mainly inciting behaviour in response to the presence of other males. Females either swam at, threatened or rushed at their mates which stimulated them to attack other males. Similar unritualised agonistic behaviours were observed as inciting behaviour in paired female Ruddy Ducks in California (Gray 1980).

Ruddy Ducks were involved in most intraspecific interactions during brood-rearing. The

rate of interaction in brood females was more than three times that of displaying males. As in Pintail (Rushforth Guinn and Batt 1985), all intraspecific interactions were initiated by brood females. Most interactions at MSWNR were directed at males, the level of aggression depending on the familiarity of the male. Females would show less tolerance and a subsequently higher level of aggression towards unfamiliar males. Aggression towards familiar attending males was mainly inciting behaviour in response to the presence of other males. Most intraspecific interactions of brood females in Utah also involved male Ruddy Ducks (Joyner 1977), but the rate of intraspecific interaction was less than that observed at MSWNR (Table 5.16).

The rate of intraspecific social interaction initiated by Pintail brood hens in Manitoba (Rushforth Guinn and Batt 1985) was 8.5 times less than the rate of those initiated by brood female Ruddy Ducks in Utah (Joyner 1977) and nearly 14 less than the rate of intraspecific interaction initiated by brood females at MSWNR (Tables 5.16 and 5.18). Brood female Bufflehead in British Columbia initiated intraspecific interactions at a similarly low rate to brood hen Pintail (Savard and Smith 1987). In the same study, brood female Barrow's Goldeneye were noticeably aggressive, but still only initiated intraspecific interactions at less than half the rate of brood female Ruddy Ducks at MSWNR. Hence brood female Ruddy Ducks initiate intraspecific interactions at a higher rate than the three species of anatid for which there are comparable data.

There may be three reasons for this.

1. Ruddy Duck brood females may be more aggressive than other brood hens *per se*.

2. Other brood females are not usually accompanied by males while male accompaniment is common in Ruddy Ducks and occurred in all birds at MSWNR.

3. Males in the other species cease reproductive activity and desert females with broods to begin the prebasic moult whilst male Ruddy Ducks remain in reproductive condition during brood-rearing and continue to attempt to rape females at this time.

TABLE 5.18. Rate of social interaction in ducks and coot during the breeding season.

Species	Reference	Time of Year	Age/sex Class	Type of Interaction	Total Number of Interactions	Length of Observation (Hrs)	Rate of Interaction (SI/hour)
Pintail	Rushforth Guinn and Batt (1985)	Jun-Aug 1979	Brood Females	All	180	96.6	1.86
				Interspecific	132	96.6	1.37
				Intraspecific	46	96.6	0.50
Bufflehead	Savard and Smith (1987)	Summer 1982	Brood Females	All	160	130	1.23
				Interspecific	107	130	0.82
				Intraspecific	53	130	0.41
Barrow's Goldeneye		Summer 1982	Brood Females	All	1377	275	5.01
				Interspecific	539	275	1.96
				Intraspecific	838	275	3.05
American Coot	Ryder (1959)	Mar-Aug 1956	Adults	Interspecific	203	139	1.46
		Mar-Aug 1957			509	220	2.31

5.5.3.2 Interspecific Interaction

In this study, Ruddy Ducks showed a very low rate of interspecific social interaction during the winter, although the rate of interaction was actually lowest during the male courtship period (Table 5.16). However, taking into account that only one interspecific interaction (in 111.3 hours of observation) during the winter was initiated by a Ruddy Duck then it becomes apparent that Ruddy Ducks were least aggressive towards other species during the winter. Siegfried (1976) also found that Ruddy Ducks were seldom involved in aggressive encounters during the non-breeding season. During winter, Gadwall and paired female Barrow's Goldeneye showed a similarly low rate of interspecific interaction to Ruddy Ducks (Tables 5.14 and 5.17a) whilst the rate in paired male Barrow's Goldeneye was considerably higher (Paulus 1983; Savard and Smith 1987). This difference was caused by the territorial wintering behaviour of paired male Barrow's Goldeneye.

Two other studies have documented interspecific social interactions during the winter. Bergan (1986) found that Ring-necked Duck, Lesser Scaup and Bufflehead on a reservoir in South Carolina were involved in interspecific interactions at exceedingly low rates (Table 5.17a). In contrast, Alexander (1987) showed that Canvasback, Redhead, Ring-necked Duck and Lesser Scaup in coastal South Carolina showed much higher rates of interaction (Table 5.17b). Bergan attributed this difference to the density of waterfowl on the coastal habitat being three orders of magnitude higher than on the reservoir. The density of wintering ducks at CVL was similar to that in Bergan's study which may partially explain the equally low levels of interspecific aggression observed in Ruddy Ducks at this time of year.

Although the number of interspecific interactions involving male Ruddy Ducks during the courtship period at MSWNR was very low, males initiated and won most interactions, therefore it is likely that males were dominant over most species at this time of year. The low level of interspecific interaction was probably a consequence of the low number of birds of other species present and the male Ruddy Duck's inclination to associate intraspecifically, both with females and other males, at this time of year.

The highest rate of interspecific interaction occurred during the brood-rearing season. The rate of interspecific interaction in brood female Ruddy Ducks was more than 25 times the

rate in courting males at the same site (Table 5.16). The number of species interacted with also increased from 6 to 21 and included all species of waterbird present on the lakes. Most interactions involved Coot or Mallard, the two commonest species on the lakes. American Coot *Fulica americana* were also involved in most interactions with brood female Ruddy Ducks in Utah (Joyner 1977) where Ruddy Duck-American Coot interactions occurred more frequently than expected from the relative abundance of the two species (Ryder 1959). Breeding female Blue-billed Ducks *Oxyura australis* have also been reported to attack Coot (Frith 1982).

Brood female Ruddy Ducks initiated the great majority of interspecific interactions at MSWNR and in Utah (Joyner 1977). Similarly, Pintail brood hens initiated 95.1% (98/103) of interspecific interactions (Rushforth Guinn and Batt 1985). All brood female anatids probably initiate brood defence in this way, therefore initiation of interspecific interactions does not provide a reliable measure of the relative level of aggression or brood defence.

Given that brood female anatids win the majority of interspecific interactions, a more accurate measure can be obtained from the rate of interaction. From the available literature, it appears that the rate of interspecific interaction in brood female Ruddy Ducks is the highest of all ducks and coot (Tables 5.16 and 5.18). The rate at MSWNR was less than in brood female Ruddy Ducks in Utah (Joyner 1977), but nearly three times that of brood female Pintail in Manitoba (Rushforth Guinn and Batt 1985). It was also nearly five times the rate of interspecific interaction in brood female Bufflehead (Table 5.18) and double the rate in brood female Barrow's Goldeneye in British Columbia (Savard and Smith 1987) and breeding American Coot in Utah (Ryder 1959).

The high level of interspecific aggression in brood female Ruddy Ducks is emphasised by the fact that they initiated interactions against species which could not have posed any danger to their young or provided any competitive threat, such as Lapwing, Feral Pigeon *Columba livia*, Blackbird *Turdus merula* and Rabbit *Oryctolagus cuniculus*. Species were threatened regardless of size if they approached broods, for example, female 1 was seen Hunched Rushing at a Canada Goose. Another example of the highly aggressive nature of brood females occurred on 24 June 1989 when female 4 was observed actually jumping out of the water while attempting to attack a Moorhen which was about 0.5m above the

female in a stand of rushes.

This aggressive nature and high degree of brood defence is characteristic of brood female Ruddy Ducks in North America (Joyner 1975, 1977), although Ladhams (1977) stated that Ruddy Ducks at CVL never defended their young against attacks from predators.

The fact that brood female Ruddy Ducks appear to exhibit a higher rate of interspecific interaction than other ducks and coot may suggest that they are one of the most aggressive species of waterbird, but not necessarily the most dominant. Of the species which regularly occurred with brood female Ruddy Ducks at MSWNR, there was a notable reduction in the percentage of interaction wins against Great-crested Grebe, Pochard and Goldeneye, although Pochard never initiated interactions against females. At MSWNR it appeared that Great-crested Grebe and Goldeneye were dominant over Ruddy Ducks. Both species are known to be aggressive, especially during brood-rearing (Cramp and Simmons 1977) and Great-crested Grebe have been observed to show aggression towards male Ruddy Ducks in Tayside (B. Thomas in litt.). The dominance and aggression of brood female Goldeneye was unequivocally demonstrated on 12 June 1988 when a female killed a four day-old Ruddy duckling from the brood of female 1.

Brood females were usually dominant over all other species except Heron, Greylag Goose and Canada Goose which mostly did not react to the females' threats. However, the situation was not as clear cut when young were present because the species with young was usually more aggressive and consequently dominant. Brood-rearing Coot at Middleton Lake, Warwickshire were dominant over Ruddy Ducks (V.E. Davies in litt.) and at MSWNR, Little Grebe, Coot and Mallard accompanying young were all dominant over Ruddy Ducks. However, the situation was reversed when Ruddy Ducks were rearing broods. The relatively late breeding season of Ruddy Ducks effectively causes two peaks of social interaction involving Ruddy Ducks during the breeding season, an early peak when other species have young and are dominant and one later when Ruddy Ducks have young and are dominant. This change in dominance has been observed between American Coot and Ruddy Ducks in North America (Ryder 1959), but Joyner (1977) observed adult American Coot to be dominant over brood female Ruddy Duck at all times.

Savard and Smith (1987) considered four hypotheses to explain the high level of

interspecific aggression in Barrow's Goldeneye:-

1. Deterrence of predators.
2. Exclusion of competitors for food.
3. Sexual selection (male interspecific aggression is assessed by females as a measure of fitness).
4. Misdirected intraspecific aggression.

They concluded that the defence of the goldeneye's invertebrate food supply was an important function of interspecific aggression, but they could not reject the possibility of misdirected intraspecific aggression.

It is possible to apply all four hypotheses to interspecific aggression in Ruddy Ducks at MSWNR. A combination of hypotheses 1 and 2 may best explain the reason for the extremely high level of interspecific interaction in brood females. Brood females attack or threaten potential predators hence hypothesis 1 may be important and hypothesis 2 may apply as many waterbirds feed on the same aquatic invertebrates as Ruddy Ducks, especially chironomid larvae, during the breeding season. It seems likely that Ruddy Ducks compensate for the limited duration of parental care, with ducklings at MSWNR abandoned at 17-22 days of age (section 4.4.1), with an increased level of parental care, in the form of defence of food reserves and physical protection from predators, during that time.

An intraspecific dominance hierarchy in male Ruddy Ducks exists during courtship, in which dominant males successfully pair with receptive females. This suggests that female appraisal of male fitness is an important component explaining intraspecific aggression in male Ruddy Duck and it is conceivable that interspecific aggression in courting males is simply an extension of that intraspecific interaction. Competition for limited suitable breeding habitat should also be considered as a reason for interspecific aggression in Ruddy Ducks in early breeding season, especially with Little Grebe which are territorial and prefer identical breeding sites.

Ruddy Ducks of both sexes could be described as superficially resembling grebes, indeed they are well known for their grebe-like awkwardness on land (Palmer 1976). However,

the applicability of this hypothesis is questionable.

Although Ruddy Ducks appeared to be dominant over most species of waterbirds at MSWNR, there was little evidence of serious competition or any detrimental effect on breeding success. Courting male Ruddy Ducks have been observed chasing Little Grebes from their nests (J. Parkinson pers. comm.), but such behaviour seems exceptional. In other parts of Great Britain, observations of aggression by Ruddy Ducks against other species are rare, but there is some cause for concern as most reported competitive interactions have involved Black-necked Grebe *Podiceps nigricollis*. On three sites in the Borders and Tayside regions of Scotland, male Ruddy Ducks have been observed Hunched Rushing at Black-necked Grebes (A. Brownhall in litt.; K. Shaw in litt.; B. Thomas in litt.). Male Ruddy Ducks were the initiator and victor of all 13 interactions reported. In contrast, a Black-necked Grebe in Fife was observed to continually attack two male Ruddy Ducks (H. Bell in litt.).

It appears that, because of the similar habitat requirements of Ruddy Ducks and both Black-necked and Little Grebes during the breeding season, a limited amount of social interaction does occur at present. However, three factors may reduce direct competition.

1. Breeding Phenology. On a temporal basis, competition will be reduced between grebes and Ruddy Ducks by the different breeding phenologies of the two species with grebes tending to breed earlier than Ruddy Ducks.
2. Limited Dietary Overlap. The overlap in food preference during the breeding season appears to be sufficiently narrow as to provide negligible competitive interaction, grebes tending to specialise on larger motile aquatic insects whilst Ruddy Ducks prefer chironomid larvae.
3. Restricted Territorial Behaviour. Black-necked Grebes and Ruddy Ducks are non-territorial during the breeding season (Cramp and Simmons 1977) and the limited territorial behaviour is restricted to the area around the female or nest, thus both species may well be able to nest together without serious competitive interaction. This factor will not apply to Little Grebes which are highly territorial during the breeding season.

Further evidence that, at present population levels, there is little serious competition

between Black-necked Grebes and Ruddy Ducks comes from Loch of Kinnordy, Tayside (B. Thomas in litt.). Even though Ruddy Duck aggression has disrupted Black-necked Grebe courtship at the site, the breeding populations of both species continue to increase and there appears to be no reduction in the reproductive performance of either species.

There have been limited observations in Great Britain of social interactions involving Ruddy Ducks and other species. Ruddy Ducks have been reported to initiate and win interactions against Mallard, Pochard, Coot and Tufted Duck (Ladhams 1977; E. Maugham in litt.; D. Murfitt in litt.; A. Shephard in litt.; B. Thomas in litt.).

In conclusion, brood female Ruddy Ducks are undoubtedly one of the most aggressive species of waterbird in Great Britain and courting males appeared to be dominant in most interspecific interactions, yet there was little evidence of direct competition with other species or any detrimental effect on their breeding success. At MSWNR, Ruddy Ducks did not appear to exclude other species from breeding areas and usually only threatened birds which approached their broods. It is possible that in such an early stage of their colonisation of Great Britain, Ruddy Ducks are still establishing themselves in the natural interspecific dominance hierarchy and that, in time, the situation will stabilise. However, as the population of Ruddy Duck in this country continues to increase (Hughes 1991) and suitable breeding sites approach carrying capacity, the potential for direct competition with species such as grebes, which prefer identical breeding habitat, will increase.

CHAPTER SIX.

GENERAL CONCLUSION.

6.1 The Ruddy Duck in Great Britain

There are many examples of introduced species competing with, harming or even causing the extinction of native species, especially where predatory or parasitic species have been introduced into island ecosystems. It has been suggested that introductions account for some 19% of bird extinctions known in the world since 1600 (Fisher *et al* 1969). Introductions may be truly accidental, such as the introduction of Dutch Elm disease fungus *Ceratostomella ulmi* into Great Britain, partially accidental, such as the introduction of Mink *Mustela vison* into this country after being deliberately imported, or deliberate, such as the introduction of the Little Owl *Athene noctua* and Canada Goose.

The majority of species introduced into Great Britain, whether deliberate or accidental, have failed to establish themselves in the wild or, if they have done so, have remained confined in limited areas (UK Committee for International Nature Conservation 1979). Of 85 species of bird introduced into this country up to 1979 only 18, including Ruddy Duck, had become established and only four (Canada Goose, Red-legged Partridge *Alectoris rufa*, Pheasant *Phasianus colchicus* and Little Owl) had naturalised at all widely. The Ruddy Duck should now be added to this list.

Most avian introductions into Great Britain have had little effect on native species. Furthermore, there seems to be no evidence that introduced species have had any major rôle in the loss of indigenous species from British ecosystems (UK Committee for International Nature Conservation 1979). Ironically, conflict has only arisen between introduced species and man. The "Canada Goose problem" in this country is now well known with birds causing agricultural damage and the more usual problems associated with their use of public parks and grassland (S. Warren pers. comm.). In consequence, limited control measures are now in operation at sensitive sites to reduce numbers.

The Ruddy Duck population of Great Britain has increased at an unprecedented rate in comparison with other introduced waterfowl. Most other species either have restricted populations or have taken a relatively long time to become established. The British population of the Egyptian Goose *Alopochen aegyptiacus*, introduced in the 17th century,

only numbered 400-500 birds in 1988 and a recent estimate of the British population of Mandarin Ducks, introduced in the early 20th century, optimistically suggests a maximum of 7000 individuals (Owen and Salmon 1988; Davies 1988). Canada Geese, introduced in the 17th century, have been the most successful introduced waterbird with an estimated British population of 60,000 in 1991 (S. Delany pers. comm.). The British Ruddy Duck population now numbers some 3,500 birds. Up to 1980/81, the number of Ruddy Ducks in this country increased exponentially (Owen *et al* 1986), but the increase has since stabilised to an average of 9.4% p.a. over the last 6 years. This increase is likely to continue, as there are many suitable breeding sites in the country which are, as yet, uncolonised and many sites where breeding does occur have the potential to support more pairs. Existing wintering sites have the potential to hold more birds and suitable wintering habitat, in the form of gravel pits, is being created every year.

This study suggests that the Ruddy Duck appears to be having little effect on native British waterbirds at the present population level. Therefore the rapid increase in the numbers of birds in Great Britain may be attributed to its having exploited a previously unfilled niche in the British wetland ecosystem, that of a night-feeding, mainly insectivorous diving duck with a unique breeding strategy among British waterbirds. That is, Ruddy Ducks channel most of their reproductive effort into the pre-laying, incubation and early brood-rearing periods, males in defending their mates and females in producing a clutch of large eggs (one of the largest per unit female body weight of any waterfowl - Lack 1967; Owen and Black 1990) which give rise to relatively large, independent ducklings which, after a relatively short period of parental care, can be deserted much earlier than in other waterfowl. This breeding strategy, combined with the extended breeding season and the associated ability to renest up to four times in one breeding season (Murton and Kear 1978) and to rear two broods per breeding season (Palmer 1976; Cramp and Simmons 1977) plus the ability of females to breed in their first year (N.S. Jarrett pers. comm.), will also increase the reproductive potential of the population.

Although it appears that Ruddy Ducks are having little direct effect on native species of waterbird, it is possible that the combined effect of the aggression of Ruddy Ducks and native species, such as Great-crested Grebe, may reduce the breeding success of other species of waterbird. Unfortunately, it is impossible to study such aspects of competition and their effect on breeding success in a short term study and conclusions in this study

are simply drawn from direct observation. In addition, as Ruddy Ducks tend to breed at individual sites in small numbers, the consequences of their presence may not be immediately noticeable on a site by site basis. Therefore, as the Ruddy Duck population continues to increase, population declines of other waterbirds may become apparent at a regional or national level.

Should the Ruddy Duck begin to compete with native British waterbirds as numbers increase, the effect should soon become apparent as numbers continue to increase. The current breeding population already exceeds, and continues to increase above, that of native species with which competition may be expected, such as Black-necked Grebe and Pochard (Spencer and the Rare Breeding Birds Panel 1991; Fox 1991). In addition, because of their highly gregarious wintering habits, Ruddy Ducks may begin to compete for food resources as flocks at major wintering sites increase.

Continued monitoring of the British populations of Ruddy Ducks and other waterbirds, via The Wildfowl & Wetlands Trust's National Waterfowl Counts Scheme, is essential to assess the ultimate effect of the introduction of the Ruddy Duck on the native British avifauna.

6.2 The Ruddy Duck in Europe

As the numbers of Ruddy Ducks in Great Britain increased, there was a corresponding increase in the numbers of continental records. After the first continental record in Sweden in 1965 (Grussu and Meloni 1991), there have now been around 300 records from 13 European countries (Belgium, Denmark, Finland, France, Germany, Iceland, Ireland, Italy, The Netherlands, Norway, Spain, Sweden and Switzerland) excluding Great Britain (Grussu and Hughes in prep.). Most of these records are from France where at least 89 birds have occurred up to and including 1990 (Dubois et le Comité d'Homologation 1991). Breeding has occurred on the continental mainland at least six times: once in The Netherlands in 1977, twice in France in 1988, twice in Spain in 1990 and once in Spain in 1991. Ruddy Ducks also bred for the first time in Iceland in 1991.

In the past, several authors have expressed concern over the possible effect which the introduced Ruddy Duck could have on the native population of White-headed Duck in

Spain (Owen *et al* 1986; Smallshire 1987; Hughes 1991). In recent years, these fears have become justified. The Spanish population of White-headed Ducks has recovered from a total of only 22 birds in 1977 to about 786 in 1992 (Anstey 1989; Agencia de Medio Ambiente de Andalucía 1992), but the threat of hybridisation and competition with Ruddy Ducks now poses a severe threat their future existence. Since the first Spanish record of Ruddy Duck in 1982, there have been at least 40 records to date (Grussu and Hughes in prep.; A.J. Green pers. comm.). During the breeding season, Ruddy Ducks tend to occur together with White-headed Ducks and there have been at least nine confirmed White-headed Duck x Ruddy Duck hybrids in Spain since summer 1991 (Green and Hughes 1992; Ramos pers. comm.). The severity of the threat of hybridisation is heightened by the fact that, in captivity, first generation White-headed Duck x Ruddy Duck hybrids are fertile and can successfully interbreed and back-cross with White-headed Ducks.

Chromosomal incompatibility and sterility factors are thought to be infrequent in waterfowl resulting in frequent hybridisation (Johnsgard 1960). Furthermore, Scherer and Hilsberg (1982) found that 20% of 418 interspecific waterfowl hybrids were fertile. By hybridising with native species, introduced Mallard have already caused the extinction of the Mexican Duck *Anas diazi* as a pure species in North America and threaten to cause the extinction of the North American Black Duck and Hawaiian Duck *Anas wyvilliana* in North America and Grey Duck *Anas superciliosa* in New Zealand (Greig 1980; Gillespie 1985; Ankney *et al* 1986). These examples illustrate the gravity of the threat of hybridisation to the White-headed Duck.

Competition with the Ruddy Duck is already a serious threat to the White-headed Duck in Spain. On Rincón Lagoon, Cordóba, both hybrids and pure Ruddy Ducks have been found to be more aggressive than White-headed Ducks and dominant over males during courtship (Arenas and Torres 1992). They were also dominant over all waterfowl with which they were observed, including Little Grebe, Mallard, Gadwall, Pochard and Coot.

In view of the above information, the threat which the Ruddy Duck poses to the Spanish population of White-headed Ducks, and indeed to the global stock, cannot be overstressed. Ruddy Ducks are already controlled in Spain, but without control measures in Great Britain, the colonisation of the continental mainland will inevitably occur, with the real

danger of the extinction of the White-headed Duck. To try and prevent further spread of the Ruddy Duck into Europe, The Wildfowl & Wetlands Trust has now initiated proceedings to tackle the problem. In Great Britain, discussions are taking place involving The Wildfowl & Wetlands Trust, Department of the Environment (DoE), Joint Nature Conservation Committee, English Nature, Countryside Commission for Wales, Scottish Natural Heritage, Royal Society for the Protection of Birds, British Trust for Ornithology and the International Waterfowl and Wetlands Bureau (IWRB) to decide how best to proceed.

Following preliminary discussions between these organisations in February 1992, IWRB and DoE informed the scientific working group of the committee for the adaptation of the directive 70/409/cee to the scientific and technical progress (steering committee for the EC birds directive) of the problem. In response, the working group passed a motion recommending that the United Kingdom and Spain take immediate action to control Ruddy Ducks.

At present, the most realistic method of control appears to be selective rifle-shooting in winter, when large flocks gather on reservoirs, but this could also be augmented with egg control, trapping and shooting during the breeding season.

To conclude I would like to quote Peter Scott who, in the foreword to Lever (1977), wrote:-

"Having been carelessly responsible myself for allowing the North American Ruddy Duck to escape and build up to a small but viable population in England, I am in no position to pass judgement on others. To be sure the Ruddy Duck is decorative and apparently harmless but no-one can know what insidious effect it may have on the ecological web. I really should not have allowed them to fly out into the countryside - although they look delightful in flight."

Conservationists and aviculturalists throughout the world should heed these words and ensure that alien species are not introduced into ecosystems where they may cause harm to native species.

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